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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 86, NO. 1, PP. 1–12 JANUARY, 1959

STUDIES ON THE LIFE HISTORIES OF MARINE ALGAE I. CODIOLUM PETROCELIDIS AND SPONGOMORPHA COALITA

KUNG-CHU FAN

Much of our knowledge of the life histories of marine algae has been acquired by means of cultural studies. Plants which are morphologically entirely different have, in a number of instances, been shown to be merely stages in the life history of one alga. In discussing the importance of cultures in relation to problems in the morphology of marine algae, Papenfuss (1950) pointed out that many problems, such as the relationship between *Codiolum* and *Urospora*, are in urgent need of further study.

Jorde (1933) has produced evidence suggesting that *Codiolum gregarium*, which is the type of the genus *Codiolum* Braun (1855), is the sporophyte of *Urospora mirabilis* Areschoug (*U. penicilliformis* (Roth) J. E. Areschoug), which is the type of *Urospora* J. E. Areschoug (1866). The present study was undertaken with the purpose of establishing whether or not *Codiolum* and *Urospora* constitute alternating phases in the life history of a single alga along the coast of California. *Codiolum petrocelidis* Kuckuck and *Urospora* sp., collected at Moss Beach (San Mateo County) were studied in culture at the University of California (Berkeley). The plants of *Urospora* sp. produced quadriflagellate zoospores which again gave rise to *Urospora* plants. These plants in turn formed quadriflagellate zoospores which produced *Urospora* plants, and this cycle was repeated over and over. The spores of *C. petrocelidis*, however, produced plants that are typical of *Spongomorpha coalita* (Ruprecht) Collins. It thus became necessary to study the reproduction of *S. coalita*. As was observed by Smith (1947), the plants of this species are gametophytic. In the present study it was found that the zygotes develop into typical *C. petrocelidis*.

The water used for culture was natural sea-water which was autoclaved and enriched with nutrients in accordance with the formula of Schreiber (1930), except that steamed pond water or soil water was used instead of distilled water. The cultures were maintained under white fluorescent-light in two water baths with a temperature ranging from 14° C to 20° C.

The writer is greatly indebted to Dr. G. F. Papenfuss who suggested the subject of this investigation and under whose direction it has been carried out. Thanks are also due to Dr. J. Proskauer, Miss N. F. Cohen, Miss F. Hewitt, Mr. M. Fuller, Dr. Janet R. Stein and Miss A. J. Waters for their help in various ways.

Detailed observations on Codiolum petrocelidis. *Codiolum petrocelidis* Kuckuck is a unicellular alga that grows within the tissue of species of the

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red alga *Petrocelis*. It was first described by Kuckuck (1894) from specimens growing in *P. hennedyi* (Harvey) Batters at Helgoland. On the Pacific coast of North America, it has been reported by Setchell and Gardner (1920) as growing within *P. middendorfii* (Ruprecht) Kjellman and *P. franciscana* Setchell et Gardner. The plant body (fig. 1) is differentiated into an obovoid or ovoid vesicle and a long, slender stalk. The cell contains many nuclei and pyrenoids and one dense chloroplast. It is usually entirely buried within the tissue of *Petrocelis* at varying depths, with the stalk extending upward. The stalk is usually differentiated into two parts: a short, more or less solid portion which adjoins the vesicle and a longer and thinner portion which is usually septate. The solid portion consists of wall material. The descriptions and illustrations of the so-called "stalk" or "stipe" given by all former authors actually only represent the solid portion. The thinner portion has apparently always been overlooked because it easily breaks off when the host material is dissected for the making of microscopic preparations. It should also be emphasized that the stalk always points toward the surface of the host and not downward as figured and described by all former authors.

Infected *Petrocelis franciscana* has been repeatedly collected at Moss Beach (San Mateo County) between February and November (presumably occurring at this locality at all times of the year) and it was obtained at Point Pinos in the Monterey Peninsula[1] in August (1957).

Codiolum petrocelidis was removed from the host tissue and cultured in autoclaved sea water in Petri-dishes. Usually after several days of culture, numerous spores are formed within each *Codiolum* cell (figs. 2, 38). Each spore possesses a reddish eyespot. Under laboratory conditions, the spores are usually retained within the parent cells and germinate there. (*Codiolum* cultured in constantly aerated water does release zoospores, however; these spores attach themselves to the sides of the vessel and germinate there. The number of flagella has not been determined, but according to Kuckuck (1897, p. 397, fig. 20) the zoospores of *C. petrocelidis* are quadriflagellate.) The sporelings that develop from the spores that lie in the terminal portion of the *Codiolum* cell usually grow faster than those in the basal portion. At an early stage, many filaments can be seen radiating in all directions from the original *Codiolum* cell (figs. 3, 4, 5). Finally, the original wall and stalk slowly gelatinize and disappear. The filaments gradually increase in width toward the tip (figs. 4, 5, 36, 40). The apical cell of each filament is large and very prominent, and it divides actively. Each cell is multinucleate and has a perforated chloroplast and many

[1] In his "Marine Algae of the Monterey Peninsula", Smith (1944) mentioned that *Codiolum petrocelidis* is known from the Monterey Peninsula from only a single collection made by N. L. Gardner. However, the present writer found that this species is common at Point Pinos. Its presence or absence at a locality (if *Petrocelis* occurs there) probably coincides with the presence or absence of *Spongomorpha coalita* in the vicinity.

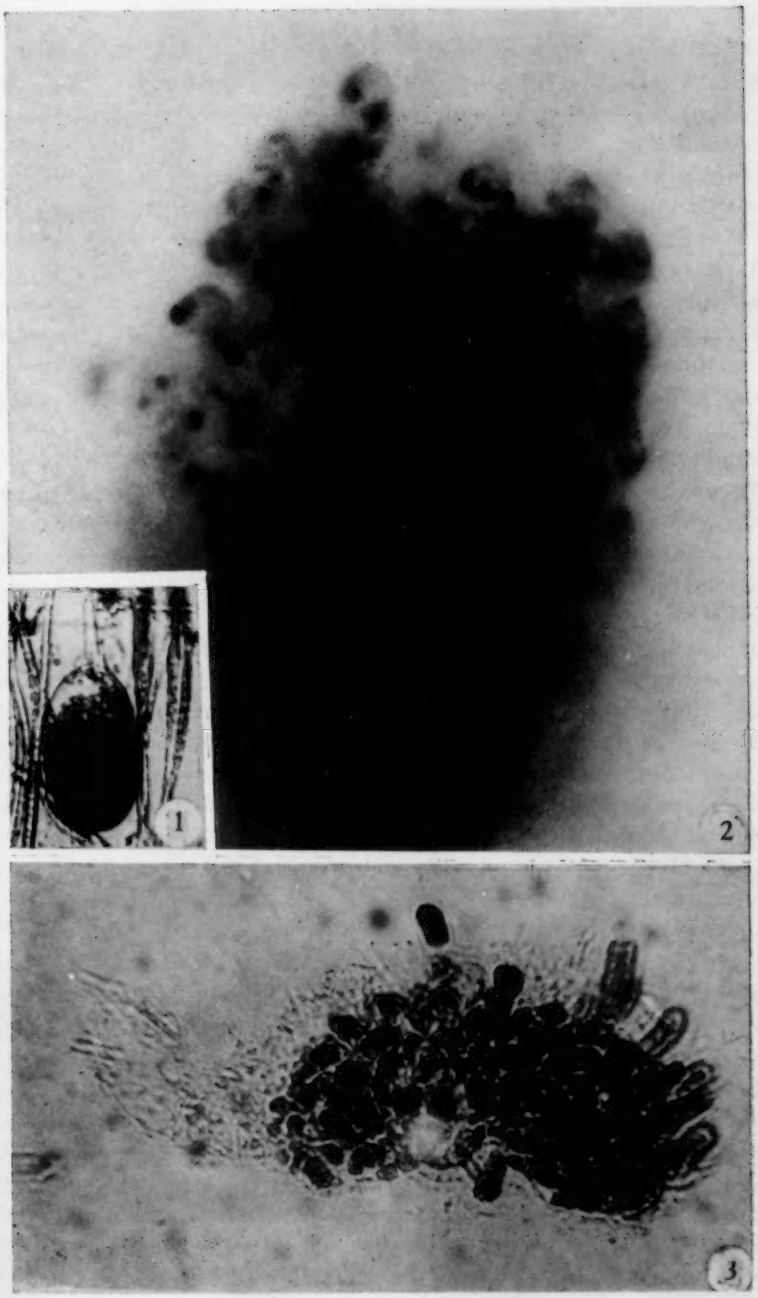


FIG. 1. *Codiolum petrocelidis* showing vesicle and solid part of stalk, the filaments which surround the *Codiolum* cell are *Petrocelis* tissue. FIG. 2. Spores of *Codiolum*, the dark spot on each spore is the eyespot. FIG. 3. Germlings (young *Spongomorpha*) produced by *Codiolum* spores. The vesicle wall and the solid portion of the stalk of *Codiolum* have gelatinized but are still evident.

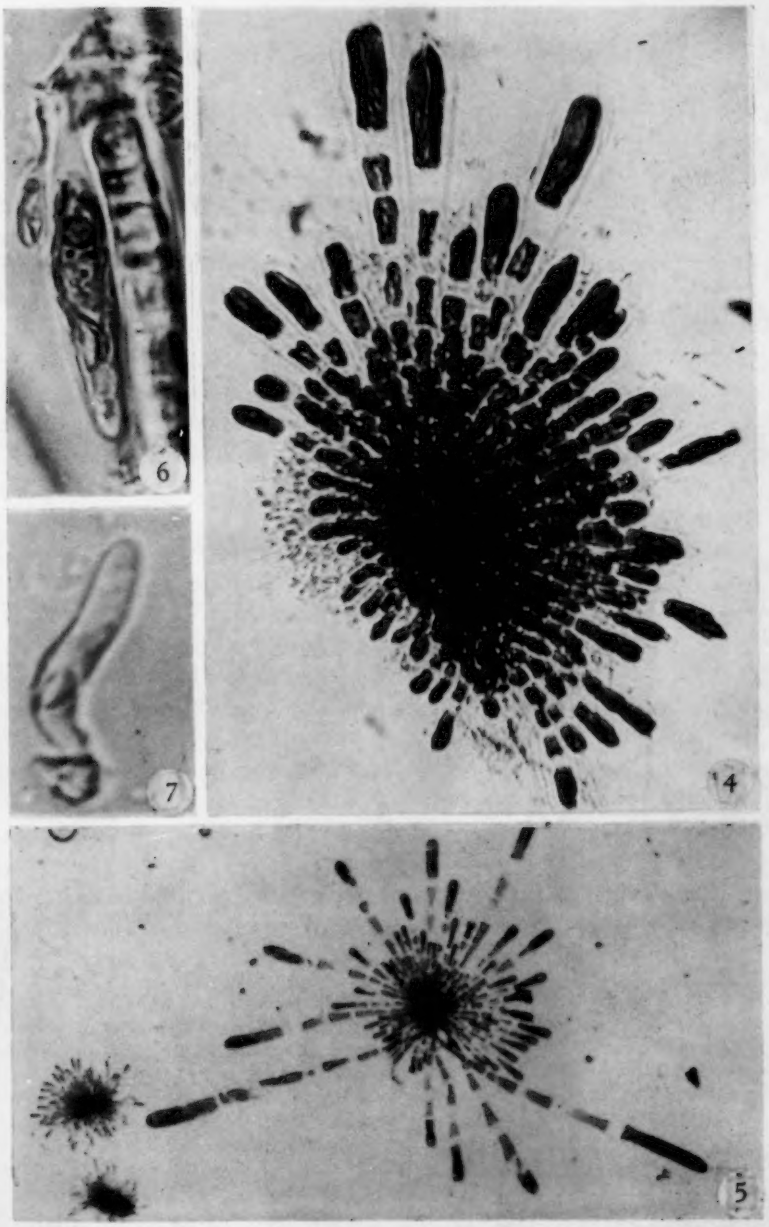
pyrenoids (fig. 40). The mass of radiating filaments continues to grow as do those thalli which were separated from it. Sooner or later, as the individual plants grow, rhizoidal branches are formed near the basal end of each filament (fig. 40). Upon coming into contact with the substratum, the tips of the rhizoids form finger-like projections by which the plantlets become firmly attached (figs. 39, 41). Plants at this stage closely resemble *Urospora*, except that in my cultures of *Urospora*, the tips of the rhizoids were never finger-like. Later, branches grow upward. The difference in size between the apical cell and the adjoining cells of the filaments gradually disappears and, at this stage, the plant strongly resembles a species of *Cladophora*. As the plants reach a height of about 1½ cm., however, hooked branchlets develop at indefinite intervals (fig. 37). These hooked branchlets branch repeatedly (fig. 37) and in due time a perfect *Spongomorpha coalita* is formed.

Detailed observations on Spongomorpha coalita. The genus *Spongomorpha* was established by Kützing (1843). Another genus, *Acrosiphonia*, which is either identical with or very closely related to *Spongomorpha*, was later established by J. Agardh (1847). For the nomenclature of these two genera, reference should be made to Setchell and Gardner (1920). Both genera belong to the Cladophorales.

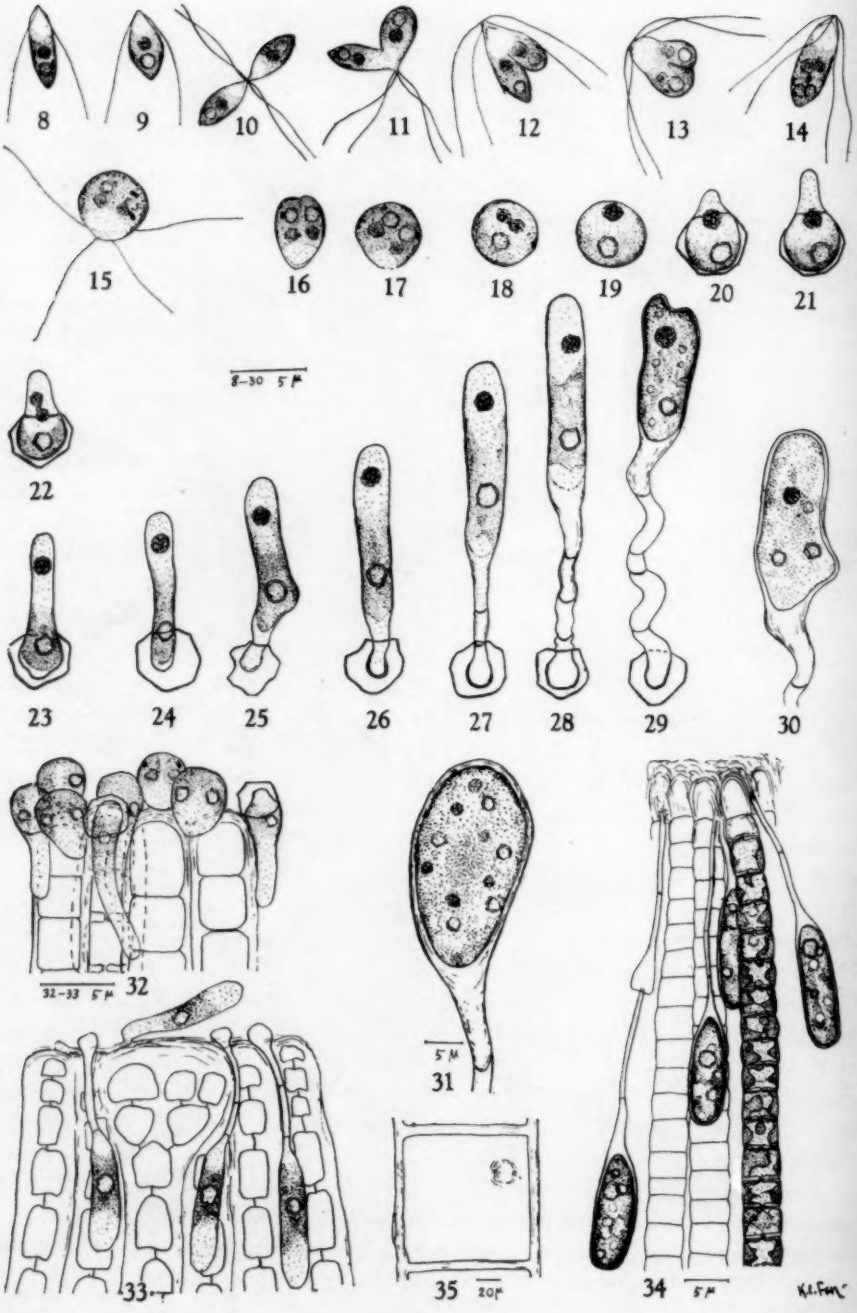
For a long time the biflagellate swarmers of *Spongomorpha* were considered zoospores (Wille, 1909). Smith (1947) showed that they are actually gametes. He concluded that *S. coalita* does not have an alternation of isomorphic generations, similar to that of certain species of *Cladophora*. Reports on the development of the zygotes of *Spongomorpha coalita* in culture have been given by Hollenberg (1957) and the writer (1957). Jónsson (1957) has described and illustrated those of *Acrosiphonia spinescens* (Kützing) Kjellman. Hollenberg's and Jónsson's results differ from those of the writer in a number of ways.

Spongomorpha coalita grows on rocks or stones in the mid-littoral belt. The plants form rope-like branching tufts about 15–30 cm. long. Hooked branchlets serve to mat together the older parts. Intercalary dark-green or brownish-black gametangia are differentiated in series or they may be separated by one or several sterile cells. *S. coalita* was collected at Moss Beach from April to October 1957 and at Point Pinos, Monterey Peninsula, in August 1957. At Moss Beach it is abundant in summer and disappears in October (1957). However, the plants of *Spongomorpha* collected in August 1957 and maintained in culture at Berkeley thrived until February 1958.

Liberation of gametes in the plants from the sea maintained in laboratory culture can be induced by slightly drying the fertile filaments and reimmersing them in water. Gametes are then discharged profusely. The behavior and the fusion of the gametes may be observed in hanging-drops, as described by Papenfuss (1935) for *Ectocarpus*. The gametes vary in



FIGS. 4, 5. Stages in the germination (young *Spongomorpha*) of *Codiolum* spores. FIG. 6. Two young plants of *Codiolum petrocelidis* (germinated zygotes of *Spongomorpha*) that have penetrated into *Petrocelis* tissue after 10 days of artificial infection. FIG. 7. Germling (young *Codiolum petrocelidis*) from a zygote of *Spongomorpha coalita*, showing the tubular outgrowth and the discarded zygote wall at the lower end.


8
9
10
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15
16
17
18
19
20
21
8–30 5 μ
22
23
24
25
26
27
28
29
30
32–33 5 μ
32
5 μ
31
33
35 20 μ
34 5 μ
K.L.Fox

shape. Typically they are spindle-shaped (figs. 8, 9). If their discharge was long protracted (or under unfavorable conditions), they usually were ovoid or even roundish.

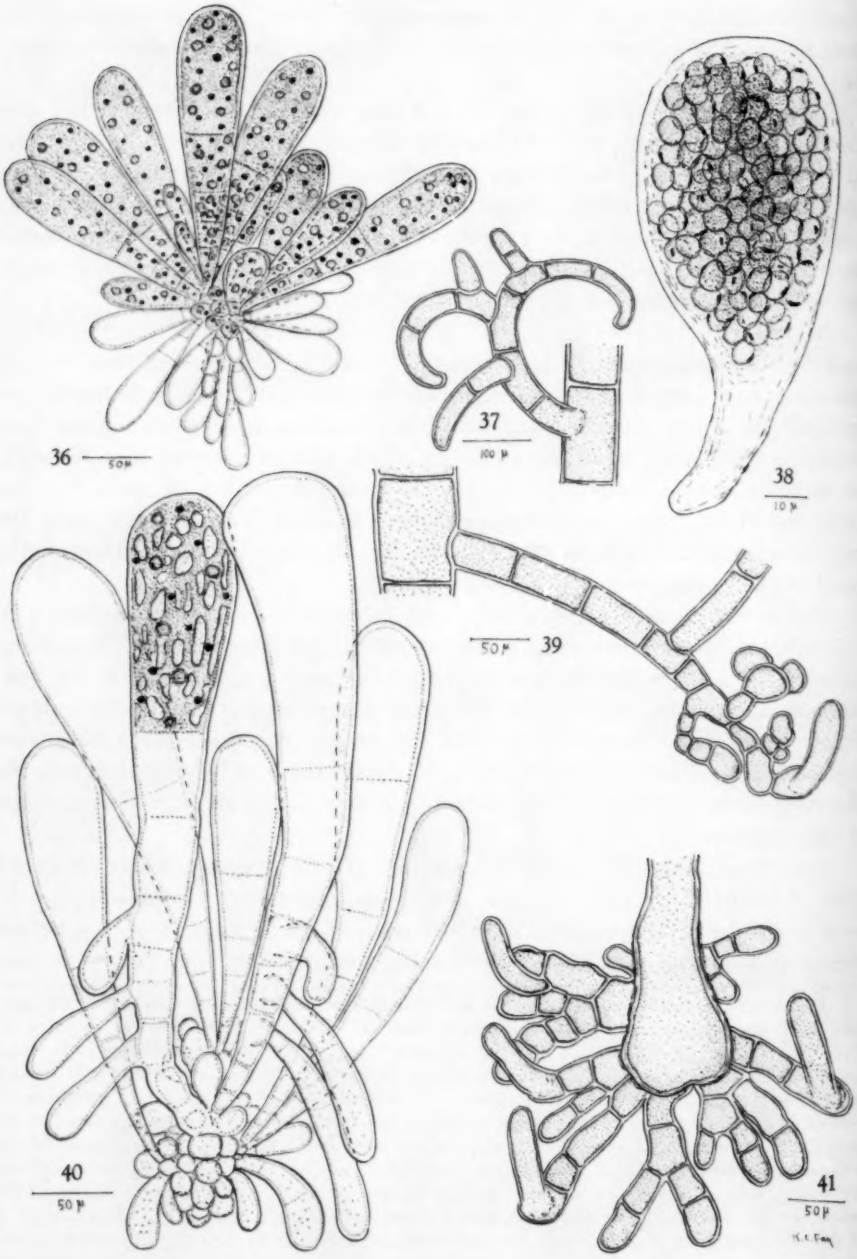
The gametes (figs. 8, 9) are 5–7.5 μ long and 1.5–2.5 μ broad, and contain a slightly oblique, more or less cup-shaped chloroplast with a pyrenoid at the posterior end. The nucleus is nearly in the center. The eyespot is very conspicuous and situated toward the posterior end of the cell. The two flagella are about twice as long as the cell and are directed backward during movement. The gametes are positively phototactic, always congregating on the side of the container that faces the light.

All my experiments have confirmed the observations of Smith (1947) that *Spongomorpha coalita* is dioecious. If two drops of water that contain gametes from plants of opposite sex are mixed, pairing of gametes can be seen within a few seconds. But no sexual reaction is seen among gametes from the same plant or of the same sex. Each pair of gametes may be equal or unequal in size. Pairing gametes first establish contact at their anterior ends and then unite. As fusion proceeds the alignment changes until the two gametes ultimately lie side by side. Usually, within a few minutes, the two cells have completely coalesced.

The newly formed zygotes have two eyespots (which remain visible up to 5 hours after the formation of the zygotes) and four flagella. They swim actively for a short time before attaching themselves anteriorly to the substratum, such as the surfaces of slides which had been placed in the culture dishes previously. They then assume a roundish form, secrete a wall, and the flagella disappear. Figures 10 to 17 show stages of fusion that may be observed from within a few minutes to a few hours after commencement of conjugation.

Karyogamy does not occur immediately after cytogamy. About 20 hours after the initial pairing, nuclear fusion and zygote germination can be seen, as shown in figures 18 to 22. The fusion of nuclei usually occurs before germination but it may also occur during germination (fig. 22). Only one

FIGS. 8–15. Gametes of *Spongomorpha coalita* and various stages in their conjugation, each gamete has a pyrenoid, nucleus and an eyespot. FIGS. 16–19. Zygotes of *S. coalita;* those in figures 16 and 17 showing two nuclei (toward lower end), two pyrenoids and two eyespots; the one in figure 18 showing union of the two nuclei and only one pyrenoid. FIGS. 20–31. Stages in development of germlings of *C. petrocelidis* derived from the zygotes of *S. coalita* (from a few hours after fusion of gametes to 24 days old), showing in figures 20–29 the zygote wall and the tubular outgrowth which becomes differentiated into a broader portion (vesicle) and a stalk; one nucleus and one pyrenoid are shown in each cell in figures 20–29 except in figure 22, in which fusion of the two nuclei of the conjugated gametes is taking place. Figure 30 is of a 14 day old germling in which one nucleus (toward upped end) and three pyrenoids are shown. FIG. 31 shows a 24 day old germling in which many nuclei and pyrenoids are evident. FIGS. 32–34. Young *C. petrocelidis* which developed from zygotes of *S. coalita* that were allowed to infect *Petrocelis* in laboratory cultures; the downward penetration of the germlings into the host tissue is clearly shown. FIG. 35. Empty gametangium of *S. coalita.*


36
50μ
37
100 μ
38
10 μ
39
50μ
40
50 μ
41
50μ

pyrenoid is visible a few hours after fusion; presumably the pyrenoid of one of the gametes disintegrates.

At germination, the wall of the zygote breaks and a tube emerges into which most of the cytoplasm flows, leaving the original zygote almost empty (figs. 20–25). The tubular projection then elongates and becomes differentiated into a broader anterior portion (vesicle) and a narrower posterior portion (stalk), which at first lies within the zygote wall. The vesicle contains the uninucleate protoplast; the stalk is more or less hyaline (figs. 25–30). The old zygote wall gradually disintegrates but is usually evident for many days. Figures 28 and 29 show 5 and 8 day-old germlings (young sporophytes), respectively. The pyrenoid remains single until the plantlets are about 13 or 14 days old; the number then gradually increases. When 14 days old (fig. 30), the vesicle is 7–13 μ wide and 10–24 μ long and still contains one nucleus. At this stage the stalk is tortuous, and sometimes it may be as long as 40 μ. The stalk is divided by septa into units of varying length. In the lower part these units are empty; just below the vesicle the stalk appears to be filled with mucilaginous material. The exact details of the formation of the stalk are as yet unknown. When 24 days old the plantlets (fig. 31) have the typical appearance of *Codiolum petrocelidis*. The vesicles then are 15–25 μ long and 10–18 μ wide, and have a multinucleate protoplast, densely filled with chloroplast, pyrenoids and reserve food.

A one month or one month and a half old sporophyte may become fertile. The zoospores which are formed again produce plants of *Spongomorpha coalita*. The development of a filamentous, branched plant directly from the vesicular stage, without formation of spores as described by Jónsson (1957) with reference to *Acrosiphonia spinescens* and by Hollenberg (1957) with reference to *S. coalita*, has not been observed in the present study.

Artificial infection of the *Petrocelis* tissue with *Spongomorpha coalita* zygotes was achieved several times. Uninfected *Petrocelis*, which was collected at Point Pinos, Monterey Peninsula, along a part of the coast where no *Spongomorpha* was present, was used in these experiments. Repeated examination established the absence of *Codiolum petrocelidis* in these plants of *Petrocelis*. Pieces of stone containing uninfected *Petrocelis* were broken into two: one part was used as a control, the other for experimental infection. The material for infection was placed overnight in large beakers containing conjugating gametes of *Spongomorpha*. Later it was transferred

FIGS. 36, 40. Germlings (young *Spongomorpha coalita*) derived from spores of *Codiolum petrocelidis* which were retained within the vesicle (the mass of radiating filaments and many nuclei and pyrenoids in each cell of the germlings are shown; figure 40 also shows rhizoidal branches forming near the bases of many filaments). FIG. 37. The hooked branchlet on a 2 cm. long thallus of *S. coalita* which was grown from a spore of *C. petrocelidis*. FIG. 38. An isolated *C. petrocelidis* (from nature) with numerous spores, each with an eyespot. FIGS. 39, 41. The finger-like projections of the rhizoids of *S. coalita* (grown in culture from spores of *Codiolum*) and erect shoots that are emerging from the rhizoidal filaments.

to a large vessel of constantly aerated sea water. The *S. coalita* used was either collected from nature or cultured from zoospores of *C. petrocelidis* in the laboratory. The results were the same. The zygotes are at first attached to the surface of *Petrocelis;* then each zygote (fig. 32) produces a projection (vesicle initial)—just as those grown on slides do. In most cases the projections extend downward into the tissue of *Petrocelis,* although some germlings may not penetrate the surface layer, but grow upward. When a germling is 4 days old (fig. 33), the hyaline basal end can still be seen on the outer surface of *Petrocelis,* but it gradually becomes indistinct. The tube-like young plantlet continues to grow downward and the vesicle becomes larger and larger (fig. 34). A four month old *C. petrocelidis* obtained from artificial infection of *Petrocelis* may attain 35 μ at the broadest part. The stalk may be long or short but is nearly always septate. No plants of *C. petrocelidis* were observed in the control cultures of uninfected *Petrocelis.*

Discussion. The results of the present study have shown that *Codiolum petrocelidis,* at least as represented on the Pacific coast of North America, is the sporophyte of *Spongomorpha coalita.* The zygote of *Acrosiphonia spinescens* (Kützing) Kjellman, as shown by Jónsson (1957), is also a spherical vesicle with a colorless rhizoid; but in contrast to the observations of Jónsson on this species and those of Hollenberg on *S. coalita,* the vesicular stage, in the writer's cultures, always produced zoospores and never directly gave rise to the *Spongomorpha* stage. It is reasonable to assume that an alternation of heteromorphic generations will be found to exist in some or all the other species of the *Spongomorpha-Acrosiphonia* complex. Whereas more than 20 species of *Spongomorpha* and *Acrosiphonia* have been described, only 3 or 4 species of *Codiolum* are recognized. Among them, only *C. petrocelidis* is reported as endophytic in *Petrocelis.* It seems likely that *C. petrocelidis* actually represents the sporophyte of several species of *Spongomorpha* (and/or *Acrosiphonia*). It would be of interest to know what the course of the life-history of *Spongomorpha* and *Acrosiphonia* is in places, such as Japan, where these two genera occur but whence *Codiolum* has not yet been reported.

Perhaps due to its small size, *Codiolum petrocelidis* has not been collected free from *Petrocelis.* Evidently it can grow independently of *Petrocelis* on other substrata, such as glass, as shown by laboratory culture. The species exhibits a marked affinity for *Petrocelis,* however, as demonstrated by the fact that in laboratory culture in association with *Petrocelis,* the zygotes usually penetrate the host surface layer, although some develop on the sides of the container.

Despite the efforts of Wille (1899, 1900, 1909) to straighten out the taxonomy of *Spongomorpha* and *Acrosiphonia,* the classification of these two genera remains confused. Wille was the first to attempt to distinguish the two genera. He restricted *Spongomorpha* to the uninucleate species and

Acrosiphonia to the multinucleate species of the complex. Setchell and Gardner (1920), Taylor (1957) and other American workers have preferred to use the name *Spongomorpha* for all the American species. Many European phycologists still use Wille's classification. *Spongomorpha coalita* is multinucleate and according to Wille's classification this alga would belong to *Acrosiphonia*, as is suggested by Jónsson (1957). However, the nuclear condition has not been studied in most species of this complex. The life-history of the majority of species remains completely unknown. Both genera include many species that lack hooked branches and that are therefore very similar to plants of *Cladophora*. A study of the life-history and cytology of the original species of *Spongomorpha* and *Acrosiphonia* probably will be helpful in solving the taxonomic and nomenclatural problems connected with these two genera.

The writer's results do not necessarily contradict Jorde's work. The fact that the species of *Urospora* which the writer cultured repeatedly produced *Urospora* may be due to seasonal differences, or the local species may have lost sexuality.

Silva (1957) has discussed the nomenclature of some of the algae with a pleomorphic life-history. As far as *Spongomorpha coalita* and *Codiolum petrocelidis* are concerned, the application of the principle of priority does not violate usage. *Spongomorpha* was published by Kützing in 1843. *S. coalita* (Ruprecht) Collins was first described (as *Conferva coalita*) by Ruprecht in 1851. *Codiolum* was published by A. Braun in 1855. *C. petrocelidis* was described by Kuckuck in 1894. So the plant which the writer has studied may be known as *Spongomorpha coalita* (Ruprecht) Collins, at least until the taxonomic problems concerning *Spongomorpha* and *Acrosiphonia* have been solved.

SUMMARY

1. *Codiolum petrocelidis* Kuckuck and *Spongomorpha coalita* (Ruprecht) Collins have been cultured in the laboratory. Wild plants of *C. petrocelidis* form zoospores which yield plants of *Spongomorpha coalita*.

2. These plants of *S. coalita* are dioecious and form only gametes, as do the wild plants. The zygotes develop into plants of *C. petrocelidis* which, like the wild plants, form zoospores.

3. Artificial infection of *Petrocelis franciscana* Setchell et Gardner with *C. petrocelidis* was achieved by using zygotes derived from plants of *S. coalita*.

4. Wild *Spongomorpha* as well as plants raised in laboratory cultures were used in these experiments. The results of this study thus show that *S. coalita* and *C. petrocelidis* represent the gametophytic and sporophytic generations, respectively, of an alga which for the present may be known as *S. coalita*.

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THE EPIBLAST AND COLEOPTILE OF THE GRASS EMBRYO

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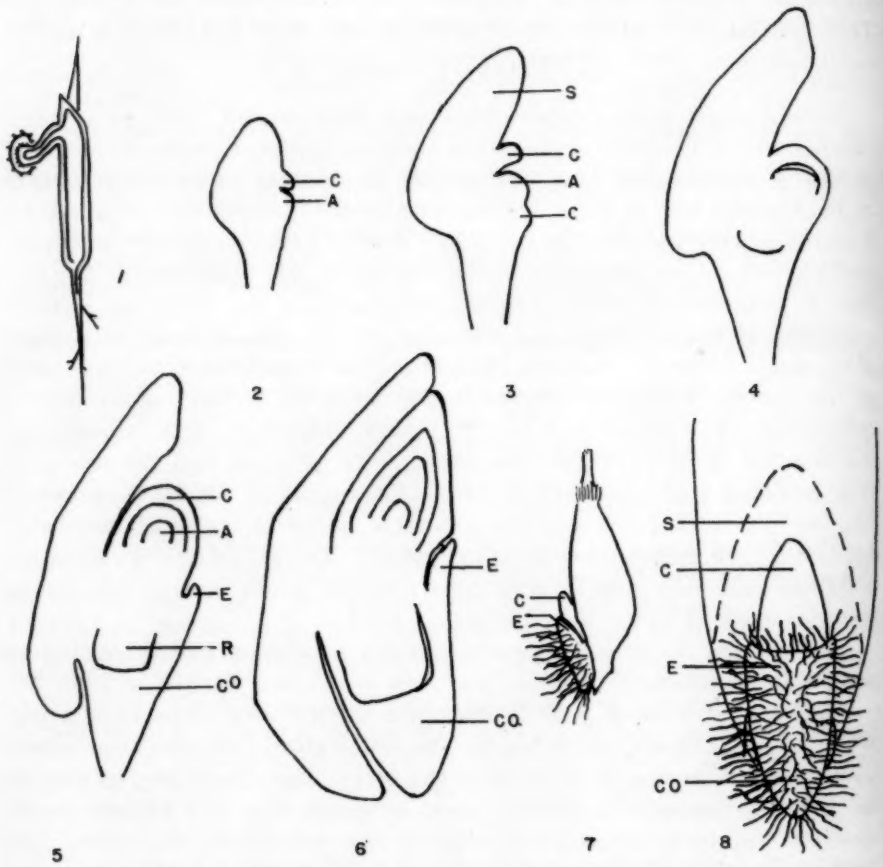
Among grass embryos some have and some do not have an epiblast (Reeder 1957). Probably more species have an epiblast than have none. The epiblast is an erect flap, long or short, has no vascular tissue, and is located on the opposite side of the embryonic axis from the scutellum (E, fig. 5–8). It has been proposed that the epiblast is a second cotyledon, a rudimentary seedling leaf, or an outgrowth of the coleorhiza. The homology of the epiblast is intimately involved with the homologies of the scutellum and the coleoptile. If the scutellum and the coleoptile are two differentiated parts of the single cotyledon, then the epiblast may be considered as an outgrowth of the coleorhiza (Goebel 1905). If the coleoptile is homologous with a foliage leaf, the epiblast may be a cotyledon, outgrowth, or a rudimentary seedling leaf. Most recent interpretations have proposed that the coleoptile is a modified leaf (Roth 1955, 1957; Reeder, 1953, 1956) or prophyll (Jacques-Felix 1957–58) and the epiblast a rudimentary second cotyledon (Roth 1957) or rudimentary leaf. In contrast, Merry (1941) considered the scutellum and coleoptile as structures peculiar to the embryo and in no sense homologous with foliage leaves.

The present discussion supports Merry's conclusion and extends it to include the epiblast.

Among Dicotyledons and Monocotyledons, the cotyledons have a different origin than do foliage leaves. The latter always develop from apical meristems, the former directly from the proembryo. Therefore, cotyledons are not homologous with foliage leaves although they may become photosynthetic organs in some species such as the castor bean and onion. The primary function of the cotyledon is secretion of enzymes and absorption of food. Merry cited the Oxford English Dictionary as follows: "Cotyledon was first used in the botanical sense by Linnaeus as referring to those seed leaves which are not in themselves depositories of nutrient but act as organs of absorption, in which he saw an analogy to the function of the cotyledon in the zoological sense" (lobes of the placenta in some mammals). Absorption may occur during seed development only or during seed development and during germination. The grass scutellum is always considered to be the cotyledon or a part of the cotyledon.

Cotyledons of some Monocotyledons have assumed additional functions such as photosynthetic activity and soil penetration. There are numerous examples in which the cotyledon not only functions in both absorption of

digested endosperm and soil penetration, but has differentiated a special portion for the latter function (Sargent and Arber 1915, Roth 1955: fig. 1). In the grasses the scutellum functions in enzyme secretion and food absorp-



FIGS. 1–5. FIG. 1. Seedling of *Tradescantia* having a coleoptile-like sheath containing the shoot apex at its base attached to the absorbing organ within the seed by a filament containing two vascular bundles. An example of a cotyledon with two specialized parts, one for absorbing digested food from the endosperm, the other for soil penetration. FIGS. 2–6. Developing embryos of *Tridens pilosus* a grass having an epiblast at maturity of the embryo but demonstrating the late development of the epiblast from the coleorhiza in fig. 5. FIGS. 7 and 8. Germinating grains of *Stipa* (fig. 7) and oat (fig. 8) showing coleorhizal hairs on the epiblast. A = apical meristem; C = coleoptile; CO = coleorhiza; E = epiblast; R = root tip of primary root; S = scutellum.

tion, the coleoptile in soil penetration and support of young leaves. Unlike cotyledons of other Monocotyledons the two portions of the grass cotyledon have become more or less separated one from the other by another structure peculiar to grass embryos, the mesocotyl, a very unusual "internode" inter-

callated between two parts (coleoptilar and scutellar) of the cotyledonary node. Nevertheless, both the scutellum and coleoptile originate directly from the proembryo (fig. 2 and 3) and not from the later-formed apical meristem. Neither is homologous with foliage leaves.

The origin of the epiblast also demonstrates that it cannot be either a cotyledon nor homologous with a foliage leaf. In the first place an epiblast, or similar structure, is found in no other family of Monocotyledons. If the epiblast is a rudimentary second cotyledon one would expect to find such a structure in other less specialized families. In the second place, there is no good evidence that the Monocotyledons originated from the Dicotyledons; there is no phylogenetic basis for calling up the ghost of a second cotyledon. Thirdly, the epiblast does not originate directly out of the proembryo as cotyledons always do but is an outgrowth of the coleorhiza, produced, in fact, rather late in the development of the embryo (figs. 2–6). Fourthly, at germination of many grasses the epidermal cells of the coleorhiza produce hairs similar in structure and function to root hairs. Such coleorhizal hairs have been reported on the epiblast of oats (LaRue 1936, and figs. 7 and 8) which would indicate that the epiblast is merely an outgrowth of the coleorhiza. During early germination they both have the same large-celled structure; they form one continuous tissue.

The epiblast cannot be considered homologous with a foliage leaf since it does not originate from the developing shoot apex.

It is concluded that the scutellum, coleoptile, and epiblast are structures peculiar to the grass embryo. All of these are not homologous with foliage leaves and the mesocotyl is not homologous with a typical internode. Speculation that assumes homologies (Jacques-Felix 1957–58; Reeder 1953, 1956; and others) is based on at most a few trivial data.

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SUMMARY

1. Cotyledons develop directly from proembryos. Foliage leaves originate from shoot apices. The origin of the grass coleoptile directly from the proembryo indicates that the coleoptile is not homologous with a foliage leaf.

2. The epiblast does not develop directly from the proembryo so cannot be homologous with a cotyledon, nor does it develop from the shoot apex so it is not a rudimentary foliage leaf. It does arise late in embryonic development as an outgrowth of the coleorhiza; it should be considered no more than that.

3. The scutellum, coleoptile, mesocotyl, and epiblast are not homologous with foliage leaves and typical internodes, but are structures peculiar to the grass embryo.

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STUDIES ON THERMOPHILIC ACTINOMYCETES

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Since thermophily was first described in bacteria by Miquel (1888), a voluminous literature has developed concerning the nature of thermophily as well as the physiology and morphology of thermophilic microorganisms. The review of Gaughran (1947) surveys the literature on all groups of microorganisms in which this phenomenon has been observed, and the review of Allen (1953) covers the thermophilic aerobic spore forming bacteria. Clegg and Jacobs (1953) summarize the general problem of adaptation to thermophily.

Among the Schizomycetes, only the thermophilic species of the Eubacteriales have been intensively investigated. The thermophilic forms among the other orders have been relatively neglected. Although the abundance of thermophilic actinomycetes in nature has been known since the work of Globig (1888), few investigations into their morphological development and physiology have been conducted. In his monograph on the actinomycetes, Lieski (1921) discusses several thermophilic isolates. In the last two decades only the observations of Waksman and Erikson, later referred to, have significantly extended this treatment.

The work described herein held two objectives. The initial aim was to develop methods for isolating and culturing thermophilic actinomycetes so as to open this obscure group to systematic investigation. The second goal was to analyze the patterns of responses of these organisms to nutritional and other variables of the environment so as to provide useful information for the solution of the problems of their growth and distribution.

Materials and methods. Isolation of organisms. One hundred thermophilic actinomycete colonies were isolated from soil and dung collected in various sections of New York State and from soil of the Mount Zion section of Jerusalem, Israel. The isolations were performed as follows: five grams of soil or dung were added to 100 ml of sterile molten one per cent agar at 55° C. The agar was incubated at 55° C for one hour during which time it was occasionally agitated to facilitate the removal of the microorganisms clinging to the soil particles. A bottom layer of nutrient medium of varying composition was poured into petri plates and permitted to harden. Five ml of the soil-agar suspension were evenly distributed over the surface of each

[1] These studies were begun at Columbia University, Department of Botany, New York in partial fulfillment of the requirements for the Ph.D. degree awarded May 1957, and continued at Yeshiva College and at the Brooklyn Botanic Garden, Brooklyn 25, New York.

pre-poured plate and allowed to harden. The plates were then incubated at 55° C or 60° C for 12 to 24 hours. The surface colonies that appeared were freed from contaminating organisms by streaking over poured petri plates containing the isolation medium. Colonies that differed in size or morphology were intentionally selected. Serial dilutions of the soil and compost samples were also plated in stock agar to obtain a quantitative estimate of the number of thermophilic actinomycete spores or hyphal fragments present in a gram of soil or compost.

Maintenance of stock cultures. The isolates were transferred to duplicate stock agar slants containing per liter, 10.0 gm. trypticase (BBL), 5.0 gm. yeast extract (DIFCO), basal salts (table 1) and 15.0 gm. agar. Glucose

TABLE 1. *Composition of synthetic media used in this study. Concentrations given are for one liter of medium at pH 7.2.*

Basal Salts	Minimal Synthetic Medium A
K_2HPO_4—0.3 gm	Basal Salts
NH_4NO_3—1.0 gm	L-Glutamic Acid—0.5 gm
$MgSO_4 \cdot 7H_2O$—0.5 gm	L-Asparagine—0.5 gm
Potassium Citrate · $7H_2O$—0.5 gm	Glucose—10.0 gm
$CaCl_2$—0.02 gm	
Fe (as $Fe(NH_4)_2SO_4$)—2.0 gm	
Zn (as $ZnSO_4 \cdot 7H_2O$)—1.0 mg	
Mn (as $MnSO_4 \cdot H_2O$)—0.5 mg	
Cu (as $CuSO_4 \cdot 5H_2O$)—0.08 mg	
Co (as $CoSO_4 \cdot 7H_2O$)—0.1 mg	
B (as H_3BO_3)—0.1 mg	

Other Synthetic Media	B	C	D	E	F	G
Minimal Synthetic Medium A	×	×	×	×	×	×
Amino Acid Mix—30.0 ml	×	×	×	×	–	×
Vitamin Mix—10.0 ml	×	×	×	×	×	–
Purine Mix—10.0 ml	×	×	–	–	–	–
Pyrimidine Mix—10.0 ml	×	–	×	–	–	–

was autoclaved separately as a fifty per cent solution and added aseptically to the medium in a final concentration of 0.5 per cent. The pH of the medium was adjusted to 7.2 with KOH. The stocks were incubated at 55° C until isolates were well grown and then stored at room temperature. Subsequent extension of this study in the laboratories of the Brooklyn Botanic Gardens revealed that the addition of 10 ml per liter blackstrap molasses permitted better sporulation and pigment production of some recently isolated strains. One set of the stock cultures was covered with sterile mineral oil.

Two sets of soil tubes were also prepared. Sieved garden soil was modified by the addition of one per cent dried sheep dung and 0.5 per cent $CaCO_3$. Screw-capped culture tubes were half filled with this soil mixture, moistened

TABLE 2. *Composition of synthetic mixes used in the nutritional studies.*

Amino Acid Mix each 5.0 ml contains:	Vitamin Mix each 1.0 ml contains:
DL-Alanine—0.04 gm.	Thiamine—0.1 mg.
Glycine—0.05 gm.	Nicotinic Acid—0.1 mg.
L-Arginine HCl—0.05 gm.	Calcium pantothenate—0.1 mg.
L-Histidine (free base)—0.04 gm.	Sodium riboflavin phosphate—0.01 mg.
L-Lysine HCl—0.04 gm.	Pyridoxamine hydrochloride—0.02 mg.
DL-Isoleucine—0.005 gm.	Inositol—1.0 mg.
DL-Phenylalanine—0.004 gm.	p-Amino benzoic acid—0.01 mg.
DL-Leucine—0.005 gm.	Vitamin B_{12}—0.1 μg.
L-Tyrosine—0.004 gm.	Biotin—0.5 μg.
DL-Methionine—0.005 gm.	Folic Acid—4.0 μg.
DL-Threonine—0.01 gm.	
DL-Tryptophan—0.005 gm.	
L-Proline—0.004 gm.	
DL-Serine—0.01 gm.	
DL-Valine—0.005 gm.	
Pyrimidine Mix each 1.0 ml contains:	**Purine Mix each 1.0 ml contains:**
Thymine—0.5 mg.	Adenine—0.5 mg.
Thymidine—1.0 mg.	Adenosine—1.0 mg.
Uracil—0.5 mg.	Hypoxanthine—0.5 mg.
Uridine—1.0 mg.	Guanine HCl—0.5 mg.
	Inosine—1.0 mg.
	Xanthine—0.5 mg.
	Xanthosine—1.0 mg.

with water and autoclaved at 121° C for 18 hours. One set received a large loopful of the surface growth of the isolate and was placed in the storage cabinet at room temperature. The other set, subsequently referred to as the incubated soil stocks, was first moistened with sodium caseinate solution

TABLE 3. *Non-synthetic media used for thermophilic Actinomycetes. Concentrations given are per liter of medium at pH 7.2. All media contained Basal salts (Table 1).*

	GYE Agar	Nutrient Agar	Sodium Caseinate Sol.	Stock Agar
Trypticase (BBL)	—	—	—	10.0 gm.
Yeast extract	10.0 gm.	—	1.0 gm.	5.0 gm.
Tryptone	—	5.0 gm.	—	—
Beef extract	—	3.0 gm.	—	—
Sodium caseinate	—	—	2.0 gm.	—
Molasses (Blackstrap)	—	—	—	5.0 ml.
Glucose	10.0 gm.	5.0 gm.	1.0 gm.	5.0 gm.
Agar	15.0 gm.	15.0 gm.	—	15.0 gm.

(table 3), inoculated with the isolates, incubated at 55° C for 12 to 24 hours, and then stored at room temperature.

Nutritional studies. The difficulty in wetting the lipid layer on the sporulated aerial mycelia (Erikson 1947) and the need for reducing the

carry over of stored nutrients necessitated the use of suspension of washed vegetative hyphal fragments as inocula. Therefore, the isolate to be studied was inoculated into stock culture medium (without agar) and grown at 55° C under bubbling aeration. This produced mycelial fragments which could be treated as bacterial suspensions. Suspensions were washed three times with phosphate buffer pH 7.2, diluted to ten times original volume and used as inocula.

Inoculum could also be prepared in small quantities for non-critical nutritional experiments or for growth rate studies by growing the organisms in a shallow layer of medium (10 ml–60 ml Erlenmeyer flask). A small piece of agar bearing some spores was removed from the stock slants and placed in each flask. The spores were thus prevented from floating on the surface of the medium where they rapidly germinate to form a tough pellicle with little proliferation of vegetative hyphae.

The oxygen requirements of these organisms was satisfied in either of two ways. The organism was grown in screw-capped culture tubes (5.0 ml of medium per 16 × 12 mm tube) inclined on a tissue culture roller. Evaporation of the medium was reduced by placing a pan of water in the incubator to saturate the air with water vapor. The organism was also grown in shallow layers of medium (5.0 ml/35 ml aluminum capped Erlenmeyer flask), in a large moist chamber made by setting the flasks in a layer of water in a large pyrex pie plate and inverting a similar pie plate over the flasks.

Specific criteria were employed for determining the adequacy of a nutritional environment. A medium was considered adequate if it was able to support the growth and sporulation of the organism in three successive sub-cultures. The absence of growth was recorded, after two inoculations failed to give growth on the test medium while the control inoculum to a stock agar slant grew well. Sterility-controls included in each experiment consisted of two stock agar slants that were incubated at 55° C and 37° C for four to five days. The media employed in this study, are presented in tables 1, 2 and 3.

Morphological studies. The isolates were studied morphologically to permit their classification under the system proposed by Waksman and Corke (1953) and utilized in the definitive study of Waksman and Lechevalier (1953).

Each isolate was grown on stock agar petri plates at 55° C to permit easy viewing of the colonial morphology, and slide cultures were prepared as follows: A v-shaped piece of glass tubing was put in a petri plate; two slides were placed on it and the unit was sterilized. Sterile distilled water was then poured into the petri plate until just below the level of the slides. Sterile molten agar medium was pipetted onto each slide or agar blocks cut from pre-poured plates were placed on the slides. After inoculation, the slide was inverted so that the agar surface faced the water layer. Failure to in-

vert the slide resulted in the rapid drying of the agar film. Although stock agar diluted 1:10 was suitable for these studies, it often provided too luxurious growth for easy viewing of spore arrangement. Sodium caseinate solution solidified with 1.5 per cent agar was often found to be more satisfactory. Although this latter medium is cloudy, the growing organisms soon cleared it.

Each isolate was examined for presence of aerial mycelium; width of conidia, vegetative hyphae, and aerial hyphae; arrangement of conidia on the hyphae; Gram stain reaction (Kopeloff-Beerman modification); and acid fastness (method of Ziehl-Neelsen). Staining reactions were determined on 12–18 hour cultures.

Tests of physiological characteristics of the isolates:

Hydrolysis of starch: 0.2 per cent soluble starch was added to the stock agar medium. Plates were "developed" with dilute Lugol's iodine solution.

Liquefaction of gelatin: 0.4 per cent gelatin was added to stock agar. Plates were developed by flooding with acid mercuric chloride.

Hydrolysis of casein: Sodium caseinate solution was solidified with 1.5 per cent agar and poured into plates. The clearing of the opaque agar was interpreted as caseinase activity.

Hydrolysis of fat: One per cent sterile cottonseed oil (Wesson oil) or tributyrin was added to molten stock agar in a screw cap bottle and vigorously agitated to distribute the oil evenly. The air bubbles that formed on the surface of the poured plate were removed by flaming with a Bunsen burner. The presence of lipase was evident by the clearing of the emulsion in the growth areas. After developing the plates with saturated copper sulfate solution, the appearance of green crystals of copper salts of fatty acids when viewed at 100× magnification was interpreted as a positive reaction.

Studies of growth rate: One isolate identified as *Thermoactinomyces vulgaris* was investigated. It was grown under measured aeration in a thermostatically controlled ± 0.01 C, water bath set into a two inch insulating layer of vermiculite.

A one liter, three-neck, round bottom flask was employed as a culture vessel. The center opening was fitted with a fritted glass aerator (30 mm coarse disc) set into a ground glass joint. One side opening, fitted with a ground glass stopper permitted the addition of inoculum and the removal of aliquots of the culture. The other side opening was fitted with a condenser that prevented loss of water by evaporation.

The rate of air flow was measured with a flow meter, and the air was filtered through sterile cotton-packed tubes set into the air line. Each flask contained 350 ml of stock medium without agar, and was aerated at the approximate rate of 4.0 ml per minute.

Growth was estimated as follows: An aliquot of culture medium (5–6 ml) was ground in a Tenbroek tissue grinder until a homogenous suspension

was obtained. The degree of turbidity was measured with a Klett Summerson colorimeter equipped with a no. 66 red filter. Growth data was analyzed by the method of least squares to obtain the slope of the logarithmic phase of the growth curve. These slopes, obtained at the various temperatures of growth, were plotted against the reciprocal of the absolute temperature to obtain the Arrhenius temperature characteristic of the organism (Porter 1946).

Results. The 100 organisms isolated for this study were identified as belonging to the family Streptomycetaceae (Breed, Murray and Hitchens 1948) on the basis of their production of a true, branching mycelium whose hyphae did not exceed 1.0 micron in diameter and did not spontaneously fragment into bacillary or coccoid forms. Conidia were borne singly on specialized conidiophores. The colonies were characterized by a powdery dry, lichenoid or radiating appearance.

Although several isolates failed to produce aerial mycelia when grown on some of the test media, all isolates produced aerial mycelia on one or more test or stock media. None was acid fast. Ninety-two were Gram positive; eight failed to give clear cut Gram reactions and should be considered Gram-variable. All isolates showed the *Micromonospora* type spore arrangement. Three isolates had grey colored spores; four isolates had bright yellow vegetative mycelia and spores, and the remainder had white spores. Thermophilic actinomycetes recently isolated revealed other morphological types and various pigmented varieties. The taxonomic significance of these characteristics will be reported later.

Isolations. All soils and composts tested contained thermophilic actinomycetes. Stock agar permitted the development of the largest number of colonies. Nutrient, sodium caseinate, and Difco A-C agars were not as good.

The number of colonies developing on the agar pour plates varied greatly with the sample analyzed. Some composts gave counts as high as 10^7 thermophilic actinomycete colonies per gram of compost. Soil from a potted geranium plant contained an average of 29 colonies per gram of soil.

Viability. All stock agar cultures stored under mineral oil proved to be viable after twenty months of storage. Three per cent of the stock agar cultures not covered with mineral oil were not viable after five months. The strain of *Thermoactinomycete thalopophilus* obtained from Dr. Waksman and the yellow spored isolate no. 19 showed prolonged viability when stored under mineral oil.

The plain soil stocks proved non-viable after six weeks of storage, whereas 90 per cent of the incubated soil stocks were viable after ten months of storage.

The aerated inoculum has two macroscopically discernible growth phases in broth culture. During the first 12 hours (approximately) the culture vessel fills with small growth center (puff-balls). After this time, these well

organized colonies break up to give a more homogeneous mass of mycelium. For the two strains tested (nos. 10 and 75) a difference in the viability of these two phases has been noted. Whereas the fragmented growth has been found viable for as long as four months when kept at room temperature, the "puff-ball" stage loses its viability in approximately one week. The washed inoculum prepared for nutritional studies could be used for approximately one week when kept at room temperature.

Physiological studies. All isolates tested liquefied gelatin and hydrolyzed casein. Only 8 failed to hydrolyze starch and only 16 possessed the ability to hydrolyze cotton-seed oil. Fifteen per cent of the cultures tested failed to hydrolyze tributyrin. Forty-five of the 100 isolates grew in successive subcultures on minimal synthetic A, and seventy-eight grew on complete synthetic medium B. Nutrient agar permitted the growth of forty-four isolates and glucose-yeast extract agar supported the growth of 83 per cent of the isolates.

The growth stimulating effect of specific nutritional groupings was clearly discernible. For example, vitamins proved stimulating for isolates nos. 16, 49, 63, 71, 95. Similar stimulatory effects of purines, pyrimidines, and additional amino acids have been noted. These results summarized in Table 4 will be presented in greater detail in a subsequent paper.

TABLE 4. *Analysis of nutritional requirements of 55 isolates unable to grow on minimal synthetic medium A.*

Accessory growth factor supplied	Number of isolates that grew
Amino Acid Mix	15
Vitamin Mix	7
Vitamin and Amino Acid Mixes	26
Purine and Pyrimidine Mixes	19
Complete Synthetic Medium B	51

The observation that many isolates could grow on the simpler synthetic media but not on the more complex ones emphasizes the sensitivity of these organisms to the components of the nutritional environment.

The minimal nutritional requirements of two isolates unable to grow in synthetic medium A was determined.

Isolate no. 16 required the addition of biotin, 0.5 μg per cent; thiamine hydrochloride 0.1 mg per cent; sodium riboflavin phosphate 0.01 mg per cent.

The yellow-spored isolate no. 19 required the addition of DL methionine 0.2 mg per cent; and L histidine hydrochloride 0.1 mg per cent. This isolate is one of many not reported by Waksman and Lechevalier (1953), and may be proposed as a new species after completion of the taxonomic study now in progress.

Growth rate of T. vulgaris (no. 10). Table 5 summarizes the results of

TABLE 5. *First order Rate Constants (k) and their parameters for growth of* Thermoactinomyces vulgaris.

Temp.	Duration of Observations (min)	Intercept	Slope (k)	Standard Error of Estimate of Slope	Degrees of Freedom (n-2)
45.5	300	2.42	.207	.01	4
	300	2.37	.230	.03	4
50.2	270	2.88	.553	.106	7
	300	2.67	.553	.043	7
	240	2.97	.530	.03	5
	240	3.25	.507	.134	5
	270	3.02	.484	.064	7
53.0	90	4.47	.691	.01	2
	90	4.44	.691	.007	2
54.0	100	3.81	.829	.011	3
55.0	120	3.18	1.105	.03	3
55.2	150	2.95	.944	.19	3
	150	2.76	1.036	.037	2
56.0	140	3.42	.959	.006	3
57.3	100	3.96	.714	.006	3
	100	3.96	.714	.006	3
	210	2.56	.737	.005	4
57.8	175	3.09	.645	.16	2
60.0	75	4.68	.207	.01	2

the analysis of the straight line portions of the growth curves when plotted as $\log_e$ of the Klett readings against time.

Figure 1 represents a plot of the $\log_{10}$ of the first order velocity constants (k) against the reciprocals of the absolute temperatures. The Arrhenius temperature characteristic (μ) calculated according to the following equation (Porter 1946):

$$\mu = \frac{4.6(\log\ k_2 - \log\ k_1)T_2T_1}{T_2 - T_1}$$

was approximately 33 kcal. (The constant, 4.6, is obtained by multiplying the gas constant (R), 1.986, and the $\log_e$ conversion faction 2.303.) Standard error of estimate of line of regression = 0.037. Regression coefficient = 0.166. Test of significance = $\frac{0.166}{0.037}$ = 4.6. Degrees of freedom = 7. T = less than 0.01.

Discussion. The ubiquitous distribution of thermophilic microorganisms in nature despite the infrequent occurrence of suitable environmental temperatures poses a problem that has engaged the interest of many investigators. Arrhenius (1927) postulated that they are propelled to Earth from the planet Venus whose average temperature is 47–50° C. Lieski (1921) and Imsenicki and Solnzeva (1945) considered the thermophiles as variants of well known mesophilic strains arising by stepwise or single step mutations. Globig (1888), Golikowa (1926), Miehe (1907), and others considered the few environmental conditions found in nature suitable for the proliferation of thermophiles, such as superficial soil layers heated by the sun and compost heaps, as the loci from whence they are disseminated.

For the purpose of this study a thermophilic actinomycete was defined as any actinomycete that could grow at 55° C or above. The grouping of thermophiles into stenothermophiles, eurithermophiles, and thermotolerant organisms appeared to serve no useful function so long as the interactions between temperature requirements and other environmental variables remain unassessed.

The work of Black and Tanner (1928) focused attention on the importance of the nutritional environment in permitting growth of thermophiles at elevated or reduced temperatures. Allen (1950) suggested, after analysis of breakdown products, that the ability of the organisms tested to grow at high temperatures is not due to unique metabolic pathways but could be attributed to a great capacity for regenerating proteins destroyed by heat. Gaughran (1949) has shown that the extracted respiratory enzymes of thermophiles can function below the minimum growth temperature, and that the Arrhenius energies of activation of reactions catalyzed by the respiratory enzymes are similar above and below the minimum growth temperature. The finding of Cleverdon, Pelczar and Doetsch (1949) that relatively high concentrations of growth factors are required by thermophiles places added importance on the adequacy of the nutritional environment in permitting growth at elevated temperatures. Except for the investigations of Baker, Hutner and Sobotka (1955) there are no quantitative data on nutritional requirements as a function of temperature. The report of Sizer (1941) however is most significant in this regard. He was able to demonstrate the dependence of the temperature characteristics of one enzyme system, the urea-urease system of *Proteus vulgaris,* on the constituents of the culture media.

In the course of the present study it was noted, that isolate no. 10 which grew equally well at 55° C in both stock medium and synthetic medium A, could also grow slowly on stock medium incubated at 37° C. However it was not possible to grow this organism in synthetic medium A at 37° C. It thus seems quite acceptable to postulate that the failure of obligate thermophiles to grow at reduced temperatures may be due to the inability of the investigator to supply an adequate nutritional environment.

The results of the viability studies again emphasize the importance of the nutritional environment. The discouraging statements in the literature concerning viability, such as that of Lieske (1922), "Die gewonnenen Reinkulturen verloren in ein bis zwei Monaten bei Zimmertemperatur ihre Lebensfahigkeit. Reinkulturen mit oder ohne Luftsporen an der Stelle in die Erde gegraben, von der das Impfmaterial entommen worden war, erwiesen sich ebenfalls in kurzer Zeit als abgestorben.", can best be attributed to the poor nutritional environment provided for growth. Likewise the report of Erikson (1953a) that "massive seedings are required, especially if growth

on solid media is desired'' is at variance with the findings in the present study. Inoculum that was thrice washed and diluted 1:10, satisfactorily initiated growth on both solid and liquid media.

The screening of the 100 isolates on nine different media revealed that growth of a thermophilic actinomycete must not be reported until after several successful subcultures on the same medium. An organism obtained from Dr. S. A. Waksman labelled *Thermoactinomyces thalpophilus* failed to grow on Waksman's synthetic sucrose agar—a medium that is reported by Waksman and Corke (1953) as suitable for its growth. The statement of Erikson (1952) that the thermophilic actinomycetes she studied could grow on Czapek's salts plus 1.0 per cent starch may also be questioned in view of the failure to specify whether successive subculturing on the same medium was possible. None of the 100 isolates presently studied possessed the ability to grow on this medium.

The classification of the thermophilic actinomycetes is in a state of flux. Waksman (1950) opposed the use of the generic name, *Thermoactinomyces*. He stated that ''the separation of the thermophilic forms into a separate genus is hardly justified since organisms which definitely belong to different genera would be included.'' Three years later Waksman and Corke (1953) proposed the generic name *Thermoactinomyces* to include thermophilic actinomycetes that resemble *Micromonospora spp.* in their spore arrangement but which unlike *Micromonospora spp.* possess a well developed aerial mycelium. This new genus appears in the classification system of Waksman and Lechevalier (1953) who recognized three species of this genus. Schuurmans, Olson and San Clemente (1956) have described a fourth species.

If this new genus is to be recognized, then the *Micromonospora vulgaris* studied by Erikson (1953a, 1953b, 1952) should be classified as *Thermoactinomyces vulgaris*. Erikson (1953b) regarded the aerial mycelia of thermophilic *Micromonospora* species as an expression of thermal dimorphism, and noted the failure to produce secondary growth of aerial mycelium at reduced temperatures that permitted proliferation of the primary vegetative mycelium. This observation casts doubt on the logicity of establishing a genus whose members may be reclassified into an entirely new genus if grown under varying temperatures. Two of the yellow spored isolates (nos. 39 and 83) obtained from Israeli soil failed to form aerial mycelia when incubated at temperatures under 53° C; and thus must be classified as *Thermoactinomyces* spp. when incubated above 55° C, and as *Micromonospora* spp. when incubated at 52° C. Likewise several isolates failed to sporulate on some of the test media. The importance of the nutritional environment in any proposed classification system is thus obvious.

The three species of genus *Thermoactinomyces* described by Waksman and Lechevalier (1953) are recognized on the basis of two characteristics;

color of spores, gray or white, and the production of a soluble wine or rose colored pigment when grown on glucose-yeast agar.

Schuurmans, Olson and San Clemente (1956) proposed a new species, *Thermoactinomyces viridis* which resembles *T. Monosporus* but differs in the width of the vegetative hyphae and in the production of a soluble greenish pigment when grown on nutrient agar. Since Waksman and Lechevalier (1953) do not state the temperature of incubation of the hyphae they measured, differences in hyphal measurements should not be considered significant in view of preliminary evidence with one isolate, that hyphal width may vary with temperature of incubation.

Five physiological characteristics seem to be of potential value in the classification of these organisms. The organisms able to grow on minimal synthetic medium A are sharply delimited from the more fastidious organisms failing to grow on maximal synthetic medium B. The failure to produce amylase, the ability to hydrolyze cotton-seed oil, and the inability to hydrolyze tributyrin, are of significance because of the infrequent occurrence of these properties in the isolates examined.

A technical difficulty encountered during the growth rate studies was the problem of excess foaming of the growing culture. Although under the conditions of the experiment this problem was not severe enough to necessitate the addition of antifoaming agents, two such agents were tried. Sterile mineral oil, 1.5 per cent, added to the aerated culture proved to be injurious to the growing organism. Dow-Corning Anti-Foam B, 0.01 per cent, reduced foaming without exerting any deleterious effect.

The studies of the growth rate of one isolate, *T. vulgaris,* were undertaken in order to establish a quantitative means of characterizing the thermophilic habit, and as a yardstick for comparison with published data on the kinetics of growth of mesophiles. Such a quantitative reference point is also useful in assessing the relative importance of the various factors for the growth of these thermophilic organisms.

In figure 1, the plot of the logarithms of the growth rate constants (k) against the reciprocals of absolute temperatures shows a range of temperatures, (45° C–55° C), over which a linear relationship exists. Above 55° C the rate of growth decreases very abruptly without displaying any linearity.

The Arrhenius energy of activation (μ), which is an estimate of the critical energy required to activate a unit of chemical reactants, is considered by many investigators to be of value only for simple reactions in homogeneous systems and not for the complex heterogenous processes of a cell. Thus, most published values of μ are for specific enzyme-substrate systems rather than for cell growth. Allen (1953) has directed attention to this fact by noting that, "for the growth of bacteria there are few data which are complete enough to deserve theoretical treatment."

John and Lewin (1946) presented data for the growth of *E. coli.* over

the temperature range of 20° C–40° C and calculated the Arrhenius energy of activation to be 15 kcal. Koffler, Johnson and Wilson (1947) similarly analyzed the data on oxygen consumption by cultures of *Rhizobium trifolii* over a temperature range of 15° C–45° C and reported that μ equalled 13.4 kcal.

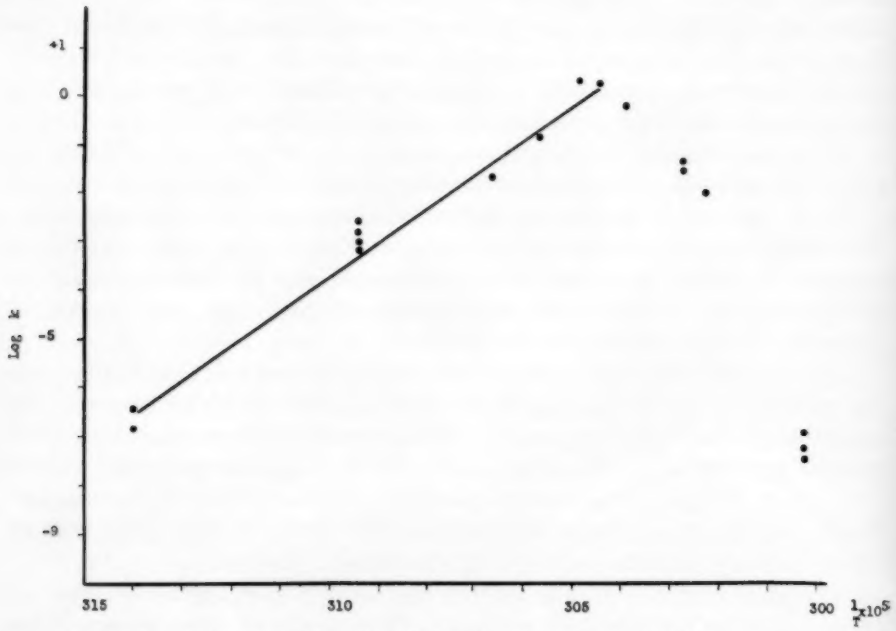

FIG. 1. *T. vulgaris* (no. 10): Growth/Temperature Characteristic.

Porter (1946) reported that most biological processes have Arrhenius energy of activation values in the range of 4 kcal to 35 kcal. Thus, the energy of activation (μ) for the growth of *T. vulgaris* under the conditions supplied, which was calculated to be approximately 33 kcal, is near the upper limit of this range. It would be highly desirable to make further comparative studies of the kinetics of growth of thermophiles and mesophiles so as to shed light on the nature of thermophily.

SUMMARY

1. One hundred thermophilic actinomycetes were isolated and obtained in pure culture. Methods are described for the maintenance and cultivation of these organisms, and for the controlled study of their nutritional requirements and growth-temperature relationships. The exoenzyme responses to varying nutritional environments and morphological characteristics are discussed.

2. Synthetic media were developed for 85 of the isolates and the minimal nutritional requirements of two isolates were determined.

3. One isolate identified as *Thermoactinomyces vulgaris* was studied to ascertain the growth-temperature relationship. Growth followed first order kinetics. The Arrhenius temperature characteristic (μ) was estimated to be 33 kcal.

Acknowledgments. The author is deeply indebted to Dr. Helen B. Funk, under whose direction and encouragement this study was begun. The help of Dr. Ray F. Dawson, Columbia University faculty sponsor of this research project is gratefully acknowledged, both for his careful direction of the growth rate studies and for his critical analysis of the entire work. The invaluable assistance of Mrs. Sifra Tendler with the mathematical calculations is sincerely acknowledged. A note of appreciation is extended to Dr. Seymour H. Hutner of Haskins Laboratories, N.Y.C., for the kind hospitality shown over the past few years enabling the author to familiarize himself with the techniques used in the study of the nutrition of microorganisms.

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CHROMOSOME BEHAVIOUR IN F_1 HYBRIDS BETWEEN SOLANUM DEMISSUM AND THREE DIPLOID SPECIES[1]

RUTH I. WALKER

Meiosis has been studied in many F_1 hybrids resulting from crosses between polyploid species in the genus *Solanum* section Tuberarium Lamm 1945, Koopmans 1951, Swaminathan and Howard 1953, Beamish, Cooper and Hougas 1957 and others. In a previous paper (1955) the author has reported partial seed sterility following crosses between *Solanum demissum* (6n = 72) and three diploid species, *S. gibberulosum* Juz., *S. tarijense* Hawkes and *S. Schickii* Juz. et Burk. The present paper is a report of the meiotic behaviour of the parents and F_1 hybrids.

Materials and methods. The following species were used in this study (P.I. numbers indicate the plant introduction numbers assigned by the Division of Plant Exploration and Introduction, U.S.D.A.)

S. demissum 2n = 72: P.I. 161725.1 and 161729.2
S. gibberulosum 2n = 24: P.I. 189215.7
S. tarijense 2n = 24: P.I. 195206.
S. Schickii 2n = 24: P.I. 189219.8
Hybrid *S. demissum* × *S. gibberulosum*
Hybrid *S. demissum* × *S. tarijense*
Hybrid *S. demissum* × *S. Schickii*

The plants were grown in the greenhouses and field plots of the Inter-regional Potato Introduction Station at Sturgeon Bay, Wisconsin during the summers of 1953, 1955 and 1957. Pollinations were made each way for each species cross. No fruits were formed following the diploid female —hexaploid cross. Meiosis was studied in the parent plants and in the representative F_1 generation. Buds were fixed in propionic alcohol (1 part of propionic acid saturated with ferric acetate and 3 parts of absolute alcohol) and were smeared and stained with propionocarmine (Swaminathan, Magoon and Mehra 1954).

Pollen counts were determined from slides stained with acetocarmine. Somatic chromosome counts were made by using root tips fixed in 0.002 M/1 solution of 8-hydroxyquinoline and smeared in 1% acetic orcein (Prakken

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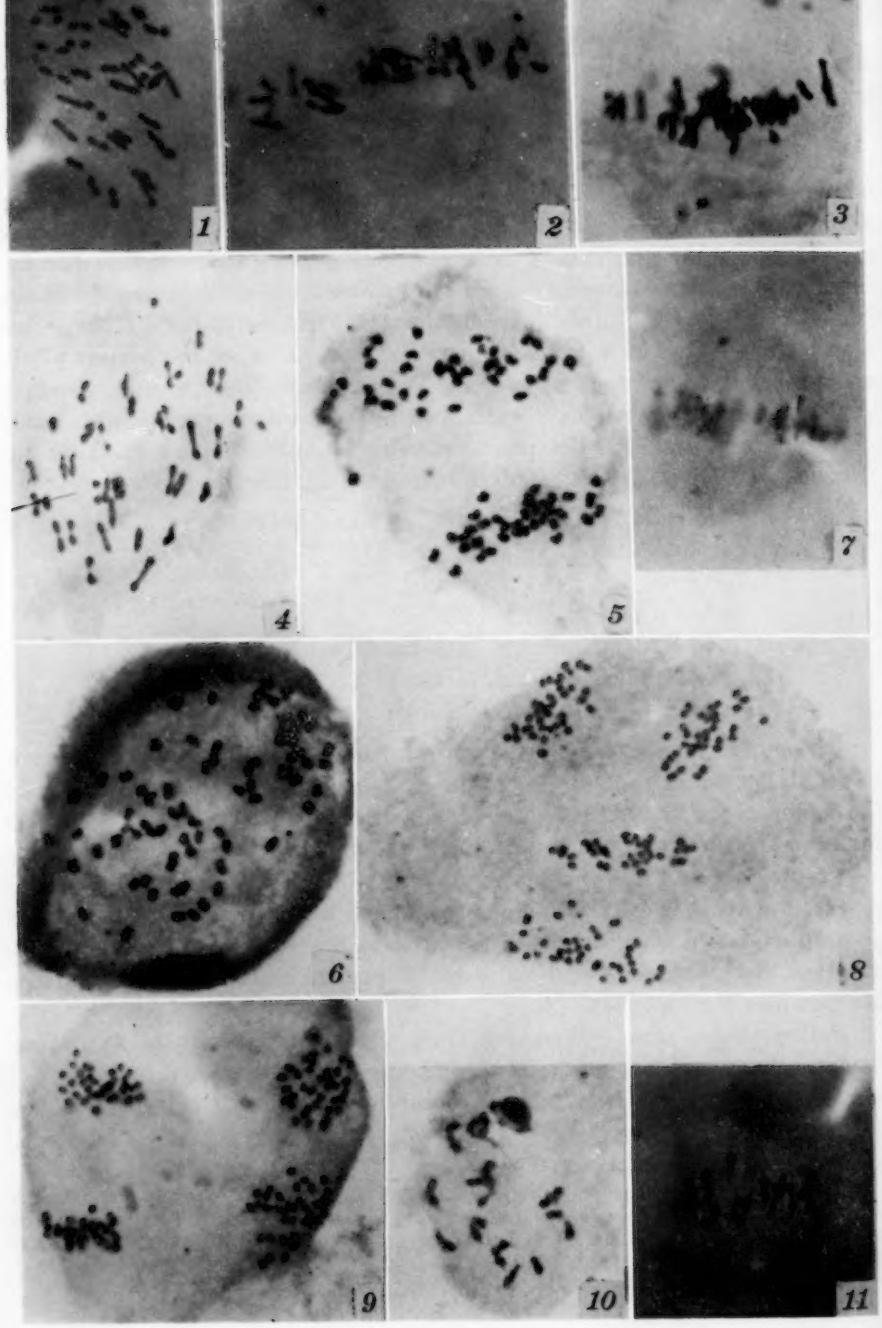
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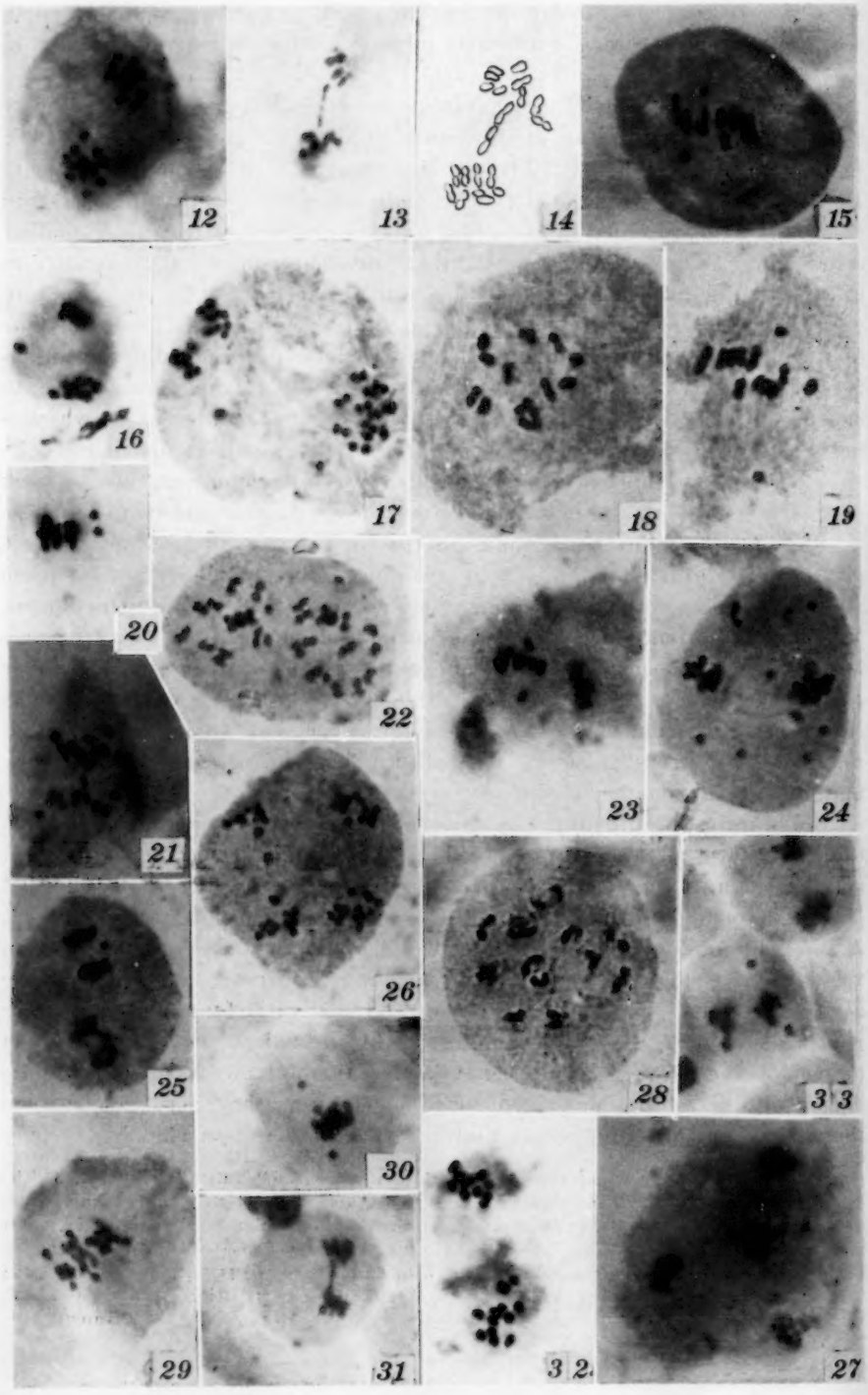
& Swaminathan 1951). Pollen grains from mature anthers were stained in a dilute propionocarmine solution to distinguish between sterile and stainable grains.

Solanum demissum. The hexaploid species *S. demissum* has previously been reported as forming 36 bivalents at first metaphase (Smith 1927, Longley and Clark 1930, Bains and Howard 1950, Swaminathan and Hougas 1954). An examination of the pollen mother cells of plants used in this experiment revealed the fact that only 47 per cent of the pollen mother cells regularly possessed 36 bivalents at first metaphase (fig. 1) whereas the remaining had bivalents and 2–6 univalents (figs. 2, 3, 4). The univalents usually occur off the equatorial plate (figs. 2, 3). The behaviour of the univalents varies during the first meiotic division; different numbers of the univalents migrate to each pole or all univalents may pass to one pole. Cells with 34 bivalents and 4 univalents are present in which 4 univalents are migrating to one pole (fig. 5). This will result in a 34:38 chromosome distribution. In other cells, two univalents migrate to each pole. The univalents split in preparation for division as shown in figure 6.

Similarly, irregularities may also occur during the second meiotic division. The univalents frequently remain off the second metaphase plate (fig. 7) and lag during their migration to the poles. In many instances, the lagging chromosomes are not incorporated in the nuclei and become lost in the cytoplasm resulting in microspore nuclei with irregular number of chromosomes as 31, 31, 36, and 38 (fig. 8). Cells with 34:34:34:38 chromosome distribution (fig. 9) are likewise present which indicates that the univalents passed to one pole at both the first and second divisions. They apparently did not divide during the second division.

Solanum gibberulosum. Twelve bivalents are usually present at diakenesis and at first metaphase (figs. 10, 11). The bivalents separate regularly at anaphase I and move towards the poles resulting in a 12:12 distribution (fig. 12). Instances of delayed division occur as shown in figures 13 and 14. A small number of the pollen mother cells examined possessed eleven bivalents and two univalents. The univalents fail to become oriented at the equatorial plate as shown in figure 15. Cells with four univalents are present, however, two of these might be interpreted as precocious division of one of the bivalents. The behaviour of the univalents during meiosis varies similar to that described for *S. demissum;* they may lag between the two groups of chromosomes and never reach the poles (fig. 16) or may

FIGS. 1–9. *Solanum demissum.* FIG. 1. Metaphase I, 36 bivalents. FIGS. 2, 3. The same with 35 bivalents, 2 univalents. FIG. 4. The same with 34 bivalents, 4 univalents. FIG. 5. Anaphase I, with a 34:38 chromosome distribution. FIG. 6. Metaphase II, polar view, 34 bivalents, 2 univalents at each plate. FIG. 7. Metaphase II, univalents off one plate. FIG. 8. Potential microspore nucleus with chromosome distribution of 31:34:36:38. FIG. 9. The same with 34:34:34:38 chromosome distribution. FIGS. 10–17. *S. gibberulosum.* FIG. 10. Diakinesis, 12 bivalents. FIG. 11. Metaphase I, 12 bivalents.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appear to have reached the poles earlier than the other chromosomes. Lagging univalents are also present during the second division (fig. 17) and will probably be eliminated from the microspore nuclei.

Solanum tarijense. Meiosis is very irregular in the pollen mother cells of this species, eleven bivalents and two univalents are commonly present (fig. 18). The univalents do not become oriented on the plate at first metaphase (figs. 19, 20). During anaphase the separated bivalents and univalents move towards their respective poles (fig. 21) resulting in a 12:12 or 11:13 distribution of chromosomes. Prior to second division the univalents divide as indicated in figure 22. Irregularities likewise occur in the second division in respect to the position of the bivalents and univalents. In some cells the chromosomes are on the spindle but are not aligned at the plate (fig. 23); in other cells, the univalents are scattered in the cytoplasm (fig. 24). During second anaphase, the divided bivalents and univalents appear to segregate unevenly between the two poles (figs. 25, 26) resulting in microspore nuclei with irregular chromosome numbers. The 11:11:11:15 chromosome distribution in figure 26 is probably the result of the two univalents passing to one pole during the first division forming an 11:13 distribution. In the second division, one of the poles of the 13 chromosome figure receives two additional chromosomes. It is assumed that the lagging chromosomes in the lower portion of the cell will eventually reach the poles. In other instances lagging chromosomes remain in the cytoplasm and are not incorporated within the nuclei (fig. 27).

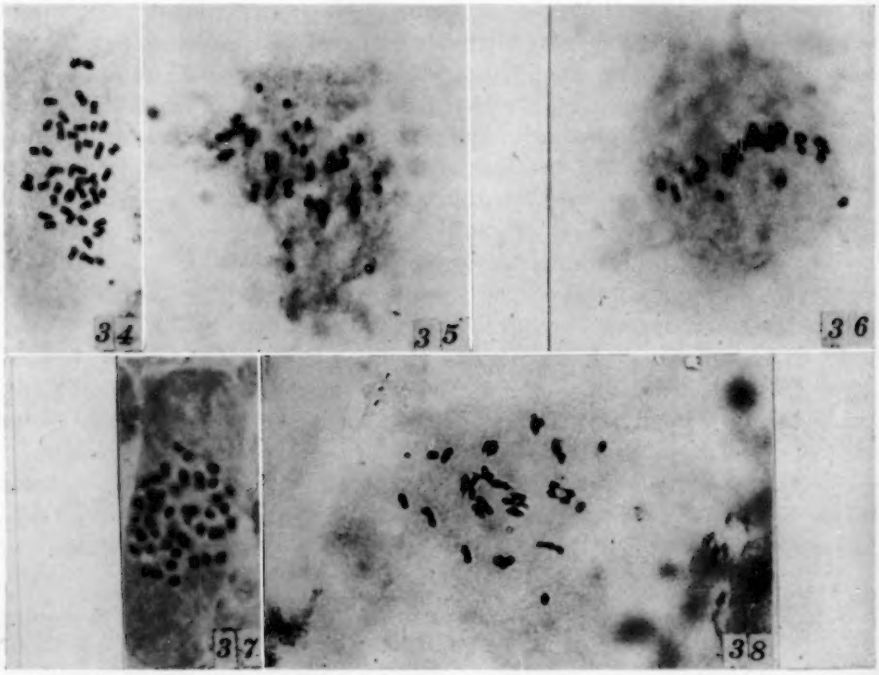
Solanum demissum × *S. gibberulosum*, *S. demissum* × *S. tarijense*. Tetraploid hybrids (2n = 48) (figs. 34, 37) resulting from these crosses show irregularity in meiosis. Varying numbers of univalents, trivalents and quadrivalents are present at first metaphase (Table 1). In figure 38 a pollen mother cell of the hybrid, *S. demissum* × *S. tarijense*, shows 20 bivalents, 1 quadrivalent and 4 univalents while figure 35, *S. demissum* × *S. gibberulosum*, shows 15 bivalents, 1 quadrivalent, 1 trivalent and 11 univalents. In no instances were 24 bivalents present. In all cases, the behaviour of

FIGS. 12–17. *S. gibberulosum*. FIG. 12. Metaphase II, polar view. FIG. 13. Telophase showing slow separation of 1 pair of bivalents. FIG. 14. Interpretive drawing of fig. 13. FIG. 15. Metaphase I showing chromosomes off the plate. FIG. 16. Late telophase of first meiotic division with chromosome laggards. FIG. 17. Second meiotic division, chromosomes in cytoplasm. FIGS. 18–27. *S. tarijense*. FIG. 18. First meiotic division, diakinesis, 11 bivalents, 2 univalents. FIG. 19. Metaphase I, univalents off the plate. FIG. 20. The same, with two univalents at the plate. FIG. 21. Anaphase I. FIG. 22. Metaphase II, polar view showing divided univalents. FIG. 23. Metaphase II with two chromosomes off one of the plates. FIG. 24. The same, showing 10 chromosomes in the cytoplasm. FIG. 25. The same, late anaphase with lagging chromosomes. FIG. 26. Early telophase II, 11:11:11:15 chromosome distribution. FIG. 27. Late telophase. FIGS. 28–33. *S. Schickii*. FIG. 28. First meiotic division, diakinesis. FIG. 29. Metaphase I. FIG. 30. Metaphase I, two univalents. FIG. 31. Anaphase I, slow separation of 1 pair of bivalents. FIG. 32. Metaphase II, polar view, 11:13 chromosome distribution. FIG. 33. Metaphase II, chromosomes off the plate.

TABLE 1. *Chromosome association of Metaphase I*

Name of Hybrid	Number of Hybrids Studied	Chromosome Number of F_1 Plants	Range of Univalents	Range of Trivalents	Range of Quadrivalents
S. demissum × *S. gibberulosum*	1	48	0–11	0–1	1–2
S. demissum × *S. gibberulosum*	1	48	1–4	0–3	1–4
S. demissum × *S. tarijense*	6	48	0–6	0–2	1–4
S. demissum × *S. Schickii*	2	60	0–7	1–6	1–12

the univalents varies, they lag, divide or remain undivided and in certain instances may be eliminated from the daughter nuclei. Univalents which



FIGS. 34–36. *S. demissum* × *S. gibberulosum*. FIG. 34. Somatic chromosome number 2n = 48. FIG. 35. Metaphase I, 15 bivalents, 1 quadrivalent, 11 univalents. FIG. 36. Metaphase I, univalents off the plate. FIGS. 37, 38. *S. demissum* × *S. tarijense*. FIG. 37. Somatic chromosome number of F_1 hybrid 2n = 48. FIG. 38. Metaphase I, 4 univalents, 1 quadrivalent, 20 bivalents. All figures ca. × 900.

lie near the poles have either passed intact to their respective poles or have never become oriented on the equatorial plate. Fragments were present which indicates that bridges may have occurred and disjoined early. The

second metaphase is almost as irregular as first metaphase. Eliminated chromosomes and fragments are visible. Defective pollen grains are numerous and the amount of stainable pollen varies from 37 to 86 per cent in different plants. Although the majority of the pollen mother cells possess 48 chromosomes, cells were observed in which the chromosome number is less than 48. This must be due to some factor which has its effect previous to diakinesis.

Solanum Schickii, S. demissum × S. Schickii. Chromosome behaviour in this species is similar to that described for *S. tarijense* and ca. 40% of the pollen mother cells possess meiotic irregularities. Twelve bivalents or eleven bivalents and two univalents are present (figs. 28, 29). The univalents do not always orient themselves on the plate at either the first or second division (figs. 30, 33). During the first division both univalents may pass to one pole (fig. 32). Delayed separation of the bivalents may also occur (fig. 31). Lagging and unequal distribution of chromosomes occurs in the second division. Matsubayshi, (1955) studying this same species obtained from seed from the Inter-regional Potato Introduction Station, Sturgeon Bay, Wisconsin, likewise found that meiosis was unexpectedly irregular, only 53.4 per cent of M-I plates examined had 12 pairs and the remaining possessed univalents ranging in number from 2 to 6.

As a result of the cross *S. demissum* × *S. Schickii* two pentaploid hybrids 2n = 60 were obtained. Pentaploid hybrids have been reported by Bains and Howard (1950), Bains (1951), Dodds (1950) and Prakken and Swaminathan (1952) following crosses between *S. demissum* and certain diploid species as *S. rybinii, S. toralapanum, S. chacoense* and *S. garciae.* Chromosome analysis of pollen mother cells of these two hybrids *S. demissum* × *S. Schickii* (2n = 60) reveals a range from 0–6 univalents, 1–6 trivalents and 1–12 quadrivalents at first metaphase (Table 1). Other pollen mother cells possessed chromosome numbers varying from 54 to 90. Irregularities at first anaphase and later stages were common, resulting in the formation of micronuclei. The pollen stainability of these two plants was 28 and 39 per cent respectively. Since dyad pollen grains are present in *S. Schickii* it is assumed that these functioned in the production of the demissum-pentaploid.

Discussion. *S. demissum* which is known to be resistant to late blight (*Phytophthora infestans*) has been used extensively as the maternal parent in various crosses with diploid species. This hexaploid species has been reported as a typical allo-hexaploid forming 36 bivalents, Howard and Swaminathan (1952). Schnell (1948) however, observed trivalents, bivalents and an occasional univalent at first metaphase. Cooper and Howard (1952) reported that quadrivalents may occur but with a frequency of not more than one per nucleus. These could be considered as "false" unions

of two bivalents. Gilles (1955) figured hexivalents and quadrivalents during diakinesis and bivalents and a doubtful quadrivalent at the end of diakinesis. He reported that chromosomes associations were extremely variable during diakinesis and was unable to state the relative frequency of the different kinds in spite of repeated observations. Further studies are to be made to determine the significance of this variability. This study showed 36 bivalents present in only about 50% of cells studied, the remaining cells contained bivalents and univalents ranging in number from 2 to 6.

Meiosis has been studied in many diploid species ($2n = 24$) and has been found to be regular, 12 bivalents being formed in nearly every cell at first metaphase although in a few cells 11 bivalents and 2 univalents occur. (cf. Swaminathan and Howard, 1953 for review of literature). Occasional irregularities such as chromatid bridges and fragments have been found in several species (Choudhuri 1943), (Lamm 1945), (Magoon, Cooper and Hougas 1958) and (Magoon, Hougas and Cooper 1958).

During the course of the present study 11 bivalents and 2 univalents were occasionally observed at first metaphase in *S. gibberulosum* and were more commonly present in *S. tarijense* and in *S. Schickii* (40 per cent of total number of cells examined). Matsubayashi (1955) has also observed univalents in *S. Schickii* in material obtained from the Inter-Regional Potato Introduction Station, Sturgeon Bay, Wisconsin. The occurrence of univalents during meiosis in various species has been considered by some investigators to be due to the precocious separation of bivalents (Swaminathan and Howard, 1953). However, Matsubayashi (1955) and Magoon, Cooper and Hougas (1958) attribute the failure of pairing to be due to segmental and genetic differences as well as other factors.

The meiotic behaviour of the tetraploid hybrids *S. demissum* × *S. tarijense* was similar with univalents, trivalents and quadrivalents present at first metaphase. With the exception of the work of Koopmans, this is in complete contrast to that of other demissum-diploid hybrids (Thomas, Vide Swaminathan and Howard 1953), Bains (1951), Howard and Swaminathan (1952) where 24 bivalents are regularly formed. Koopmans (1951), however, reported that in *S. demissum* × *S. caldasi* hybrids meiosis was irregular and lagging chromosomes often occurred. The latter were apparently lost as the numbers at second metaphase were 19, 20 and 21. Meiotic divisions were also irregular in the hybrid *S. demissum* × *S. commersonii*. Univalents varied from 0 to 5 and trivalents and quadrivalents may be present.

Pentaploid hybrids resulting from the *S. demissum* × *S. Schickii* likewise showed irregularity in chromosome numbers and in the numbers of univalents, trivalents, and quadrivalents formed. Bains and Howard

(1950), Dodds (1950) and Prakken and Swaminathan (1952) have previously reported pentaploid hybrids following crosses between *S. demissum* and the diploid species *S. rybinii*, *S. toralapanum*, *S. chacoense*, and *S. garciae*.

In the present study, the irregularities in meiosis in pollen mother cells of the tetraploid and pentaploid hybrids may be attributed to structural differences which exist between some of the chromosomes. The effect of physiological and environmental factors on the process must not be excluded.

SUMMARY

1. The meiotic behaviour of the F_1 hybrids following crosses from *S. demissum* and three diploid species, *S. gibberulosum*, *S. tarijense* and *S. Schickii* were compared with that of the parent species.

2. Twelve bivalents were usually present at first metaphase in the pollen mother cells of the diploid *S. gibberulosum* while 11 bivalents and 2 univalents are commonly present in *S. tarijense* and *S. Schickii*.

3. *S. demissum*. The female hexaploid parent showed irregularities in meiosis in that only 47 per cent of cells examined possessed 36 bivalents. Univalents varied from 2–6.

4. The 48 chromosome hybrids obtained from the crosses *S. demissum* × *S. gibberulosum* and *S. demissum* × *S. tarijense* had varying numbers of bivalents, univalents and multivalents in the pollen mother cells at first metaphase.

5. Pentaploid hybrids (2n = 60) resulted from the cross *S. demissum* × *S. Schickii*. Since dyad pollen was observed in *S. Schickii*, it is assumed that the increased chromosome number of the hybrid was contributed by the diploid parent species.

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VARIATION IN EXCISED TOMATO ROOT CULTURES

ADDISON E. LEE[1]

The culture of excised roots has become established as an important technique in plant physiological research. It also holds promise of becoming an important research technique in physiological genetics and morphogenesis.

Comparative studies of excised roots among different species, varieties, and classes have revealed distinct differences in their growth rates, morphology, and metabolism (Street 1957; Boll 1954a, 1954b; Lee 1954a, 1954b, 1958a, 1958b). Robbins (1941) and Whaley and Long (1944) have reported differences between the root cultures of two inbred tomato lines and their hybrid with the suggestion that heterosis had occurred. Boll (1954b), using the same lines but with some refinements in technique, concluded that heterosis had not occurred. However, some basic differences between the root cultures from the two parents were noted. Skinner [1952, 1953 (as cited by Street 1957)] has shown that intra-specific strains of groundsel have genetically controlled differences. Roots from F_1 generation had an intermediate growth rate while those of the F_2 generation showed segregation of the growth rate characters. The author (in press) has shown that excised roots obtained from seedlings carrying a mutation for dwarfness exhibit reduced growth in culture when compared with roots obtained from a comparable normal or non-mutated form.

Boll (1954a) reported considerable inter-clonal and test-to-test variation in his cultures and concluded that the behavior in culture of a single clone could not be taken as representative of a given inbred line. The existence of these variations does not necessarily invalidate interpretation of differences which may be found among different lines. However, their occurrence does impose certain limitations on the experimental procedure and indicates the need to explore the possibilities of locating lines and clones which might show less variation than those previously reported.

The purpose of this paper is to report the statistical analysis of results comparing the growth of several root clones, during repeated subculture, from several inbred tomato lines selected as examples of highly homozygous lines and one line which had been derived by doubling the chromosome number of a haploid. The latter was selected as representing an extreme degree of homozygosity.

[1] The author wishes to express appreciation to Mr. Harry Beck, Senior Research Assistant, Division of Educational Research, The University of Virginia for his assistance in the statistical analysis reported in this paper.

Materials and methods. For the first part of this investigation, lines designated as University of Texas 120 and 122 were selected. These were obtained in 1954 from Dr. LeRoy Powers of the Cheyenne Horticultural Field Station, Cheyenne, Wyoming. Line 120 was developed at the Cheyenne Station by Dr. Powers and Dr. D. H. Scott. It was released by the Bureau of Plant Industry, Soils, and Agricultural Engineering as the Alpine Tomato and was characterized by its early productiveness and high yield of fruit. At the time of the studies reported here it had been inbred for more than 14 generations. Line 122 is the Sioux tomato, another plant characterized by its high yield of fruit. It was introduced by the Nebraska Agricultural Experimental Station, Lincoln, Nebraska, in 1944 (Werner 1944) and has been inbred since prior to 1942.

For the second part of this investigation lines designated as University of Texas 126 and 127 were studied. These were obtained from Dr. C. M. Rick, University of California, Davis, California. Line 126 was developed from seed of the variety San Marzano carrying a single gene mutation for dwarfness. Line 127 was developed from a haploid of the same variety whose chromosome number had been doubled by colchicine (Rick 1952).

Four clones of excised roots, each derived from a single seed were developed by standard root culture techniques from each of these four lines. After five or more transfers were made to establish the roots in culture, thirty tips were harvested at each of four consecutive tip passages and the length of the main axis of each tip determined. In subculturing all of the roots a three day segment passage was alternated with a four-day tip passage. White's standard medium (1943) was used for all the cultures.

The data obtained were compared statistically using the analysis of variance technique with the level of confidence at .01 (Snedecor 1956).

Results. The mean lengths and the standard errors of the means of each clone through four consecutive passages are given in Table 1.

When line 120 was compared with line 122 by analysis of variance the two lines differed significantly at the 0.01 level (line 122 > line 120). In these two lines there were no significant differences between the clones within each line. However, there were some significant test-to-test variations during different passages of each clone. The following summary indicates the extent of the significant differences at the 0.01 level.

120 B	Passage 3 > Passages 1, 2, and 4.
120 C	None
120 D	None
120 E	Passage 1 > Passages 2 and 4
	Passage 3 > Passages 2 and 4

122 A Passage 4 > Passage 2
122 C Passage 1 > Passage 2
Passage 4 > Passage 2
122 D None
122 E Passage 3 > Passage 1, 2, and 4
Passage 1 > Passage 4

A comparison of line 126 and line 127 by analysis of variance reveals a significant difference between the two lines at the 0.01 level (line 127 > line 126). A comparison of the several clones from each line also shows significant differences. Thus in line 126, Clone D > Clones, C, A, and G. In line 127, Clone H > Clones F and C.

TABLE 1. *Growth in length (mm.) of root main axis during each of four consecutive passages. Figures represent means of thirty roots from each clone at the end of each passage.*

Line and Clone	1st Tip Passage	2nd Tip Passage	3rd Tip Passage	4th Tip Passage
120B	64.6 ± 3.8	72.4 ± 4.1	89.0 ± 2.7	62.4 ± 3.2
120C	79.4 ± 3.3	83.7 ± 4.1	79.8 ± 2.3	82.2 ± 4.5
120D	82.7 ± 5.0	76.4 ± 3.7	75.5 ± 4.3	79.5 ± 3.2
120E	88.9 ± 3.3	65.1 ± 3.5	82.6 ± 2.2	69.2 ± 2.2
122A	88.8 ± 2.7	81.9 ± 3.5	92.8 ± 3.4	96.5 ± 2.6
122C	96.6 ± 2.6	79.7 ± 2.9	87.1 ± 3.5	101.5 ± 2.7
122D	96.3 ± 2.4	94.4 ± 2.4	97.2 ± 2.9	88.3 ± 1.9
122E	89.4 ± 2.6	85.5 ± 2.7	100.8 ± 2.6	77.7 ± 2.4
126A	66.0 ± 1.6	69.0 ± 1.8	64.1 ± 2.0	64.6 ± 2.2
126C	89.6 ± 2.9	82.3 ± 3.3	86.5 ± 3.0	109.0 ± 3.3
126D	95.1 ± 1.8	97.6 ± 3.6	101.9 ± 3.6	114.4 ± 3.3
126G	61.9 ± 1.8	62.9 ± 2.4	59.7 ± 2.0	62.2 ± 2.0
127B	65.1 ± 3.0	90.7 ± 3.1	117.4 ± 2.6	118.3 ± 4.2
127C	67.5 ± 2.4	89.0 ± 3.2	98.3 ± 3.8	112.6 ± 2.5
127F	78.8 ± 3.0	110.2 ± 3.3	83.5 ± 3.5	104.3 ± 4.3
127H	74.9 ± 2.3	119.3 ± 2.8	97.5 ± 3.1	121.4 ± 2.3

Significant test-to-test variations were also noted. The following summary indicates the extent of these variations.

126 A None
126 C Passage 4 > Passages 1, 2 and 3
126 D Passage 4 > Passages 1, 2 and 3
126 G None
127 B Passages 3 and 4 > Passages 1 and 2
Passages 2, 3 and 4 > Passage 1
127 C Passage 4 > Passages 1, 2, and 3
Passages 2, 3, and 4 > Passage 1
127 F Passages 2 and 4 > Passages 1 and 3
127 H Passages 2 and 4 > Passages 1 and 3
Passages 2, 3 and 4 > Passage 1

Discussion. In a recent review on excised root culture, Street (1957) has summarized much of the literature relating to inter and intra-specific variation. It appears quite clear that many of these variations are detectable by root culture techniques and that they represent characters which can be used to distinguish different species and different varieties within a species. In fact the difference between varieties in some instances is their ability to grow or not to grow in culture by currently known techniques. The interclonal and test-to-test variation emphasized by Boll (1954a) is a more serious problem. Street points out that even moderately unfavorable growing conditions and variations in the physiological state of the inoculum could intensify the variability reported by Boll. Street also made reference to experiments in his own laboratory which were set up to study the magnitude of inter-clonal differences and how they might be related to the extent of inbreeding. Included in his experimental material was a doubled haploid. Unfortunately, Street judged his results to be inconclusive because the different lines he used proved to have different basic requirements (*i.e.* different sucrose concentrations optima) and thus not comparable for the determination of genetically controlled variation.

Line 127 (the doubled haploid) and line 126 used in the present study had the same sucrose concentration optima although they differed in some other responses (Lee 1958b). The analysis of variance showed clearly that the two lines were significantly different, however, inter-clonal variations and test-to-test within clones were as obvious in the doubled haploid line (127) as in the mutated form from the same variety (126). It should also be noted that inter-clonal variations were more pronounced in lines 126 and 127 than in lines 120 and 122.

It seems clear that the selection of stocks for higher degrees of homozygosity does not eliminate inter-clonal variation and test-to-test variation within clones. This emphasizes the importance of using highly refined culture techniques, carefully controlled environmental conditions, the repeated use of controls for each experiment, the necessity of demonstrating reproducable results, and the use of enough samples to permit statistical analysis. Thus in our present state of knowledge, we are in a position to consider differences in growth of cultured excised roots as genetically controlled only if they are of a magnitude to be statistically significant in spite of inter-clonal and test-to-test variations.

SUMMARY

1. Excised root cultures were established from four highly inbred lines of tomato. One of these was originally derived by doubling the chromosome number of a haploid. Four clones from each of these lines were established

and measurements made of main axis length made at the end of four successive passages.

2. The data were compared statistically using analysis of variance techniques. Statistically significant differences were determined between the different genetic lines.

3. Significant inter-clonal differences as well as test-to-test differences within a given clone were also found.

4. The implications of these variations in terms of culture techniques and interpretation of results were discussed.

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CORDYCEPS SPECIES

E. B. MAINS

During a study of North American species of *Cordyceps* (Mains 1957, 1958a), considerable information was obtained concerning species elsewhere, especially from South America and China. These included types of species in the Farlow Herbarium described by Patouillard, P. Hennings, Berkeley and Curtis and Petch (FH) and those of Teng in the National Fungus Collections, United States Bureau of Plant Industry (BPI). Also a number of collections from Argentina and Bolivia have been received from Rolf Singer (MICH). The results of a study of species in the Lloyd Herbarium (BPI) has been presented elsewhere (Mains 1958b).

Cordyceps parvula sp. nov. figs. 1–3. Stromatibus parvis, cylindricis, 1–1.5 mm longis, 100–200 μ latis, cinereis, pruinosis; peritheciis ovoideis, 500–650 × 250–300 μ, brunneis, superficialibus, caespitosis in apicibus stromatum; ascis cylindricis, 400–500 × 5–6 μ; ascosporis filiformibus, cellis 8–10 × 1 μ; synnematibus cylindricis, capitatis; phialidibus cylindricis, 8–10 × 2 μ; conidiis ellipsoideis, 3–4 × 1.5 μ.

On a species of Orthoptera, near Zaraza, Guarico, Venezuela, Dec. 8, 1939, C. E. Chardon, 3727, type (MICH).

The stromata are scattered, very small with the perithecia in small clusters at the apices (figs. 1 & 2). They consist of parallel or slight interwoven longitudinal hyphae with an outer covering of short, loose, flexuous hairs. The perithecia are ovoid, with acute apices (fig. 3), and are crowded but not embedded. The cylindric asci have 4 μ thick caps. The ascospores are filiform and part spores were not seen. The stromata are accompanied by synnemata which are similar to the stromata except they are slightly capitate with obovoid or globoid heads, 175 × 100–175 μ. The heads are covered by a layer of cylindric phialides. The conidia are hyaline and ellipsoid, 3–4 × 1.5 μ. The apically clustered superficial perithecia separate this species from others on Orthoptera.

Cordyceps trinidadensis sp. nov. fig. 4. Stromatibus parvis, 2 mm longis, capitatis; capitulis turbinatis, 0.8 mm latis, pallide brunneis; stipitibus 0.2 mm latis, fulvidis; peritheciis anguste ellipsodeis vel oblongis, 250–300 × 100–125 μ, apicibus rotundatis, immersis ad perpendiculum; ascis cylindricis, 125–175 × 2.5–3 μ; synnematibus albis, 1–1.5 mm longis, ramosis; phialidibus oblongis, 8–10 × 3 μ; conidiis oblongis, 6–10 × 1.5–2 μ.

On a cricket (Orthoptera) Concord Estate, Saugre Grande, Trinidad, Jan. 4, 1917, F. W. Urich, FH6162, type.

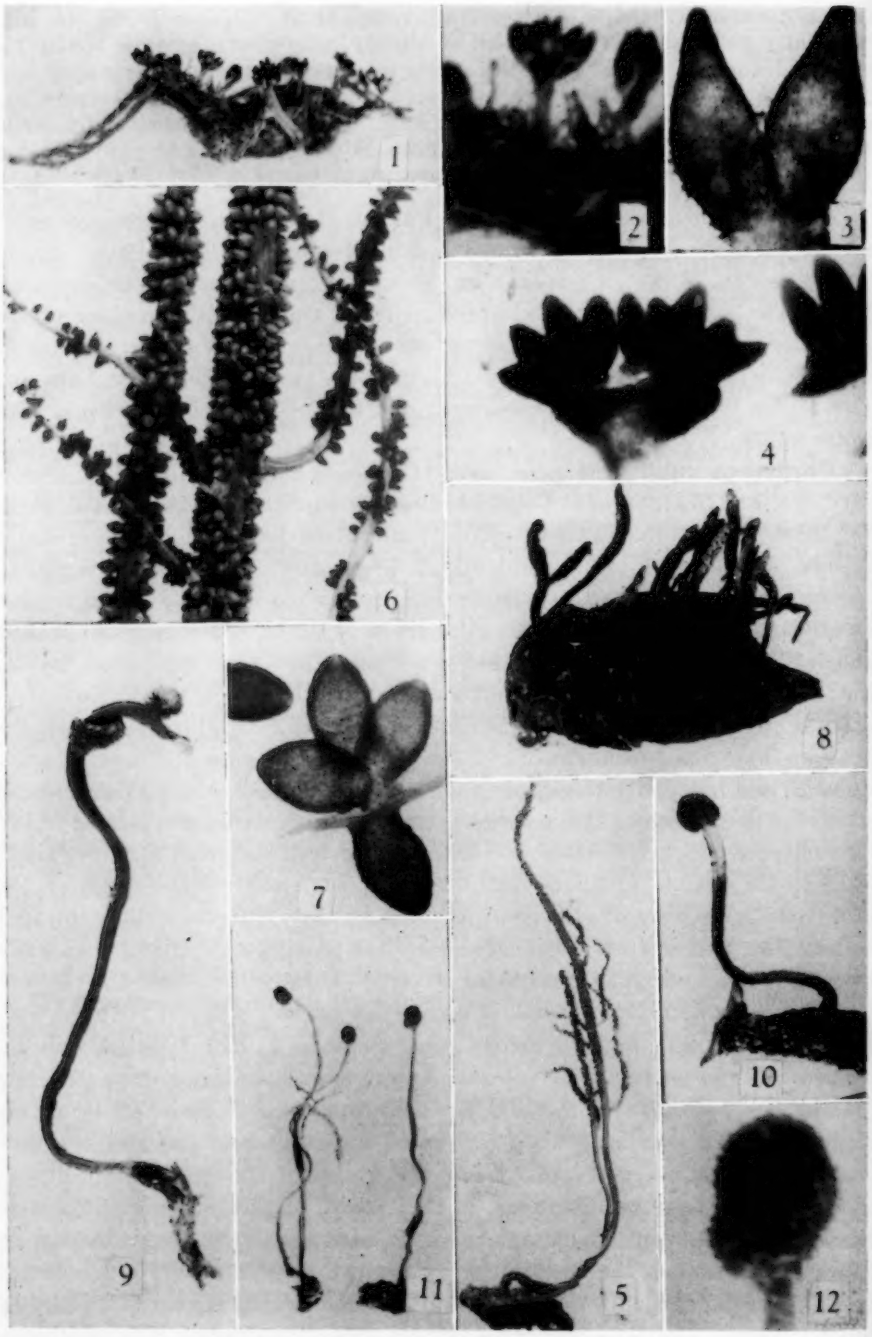
The stromata are very small only 2 mm long with flattened turbinate light brown heads less than 1 mm wide and slender, 0.2 mm thick, yellowish stipes. The stipes consist of longitudinal hyphae which spread out above and become interwoven in the base of the head. The perithecia are crowded

and are narrowly ellipsoid or oblong, rounded at the apices (fig. 4), and vertically embedded in soft tissue of closely interwoven hyphae without a differentiated cortex. The ostioles of the perithecia open on the upper surface of the head. The asci are cylindric and immature. The stromata are accompanied by white slender synnemata. The conidiophores which arise from their apices are repeated dichotomously branched and the branches terminate in oblong phialides with asperulate apices.

This specimen was found in the Farlow Herbarium determined as *C. uleana* P. Henn. by Petch. As described by Hennings (1904), Petch (1934) and Moureau (1949), *C. uleana* has much larger stromata with spherical heads. The perithecial are embedded at right angles to the surface of the head and are larger and have acute apices. *C. trinidadensis* is close to *C. langlosii* which was described from larvae of a mason wasp from Lousiana (see Mains 1958a). The latter, however, has embedded ovoid perithecia with acute apices.

Cordyceps subflavida nom. nov. (*C. albida* Pat. & Gaillard Bul. Soc. Myc. Fr. **4**: 116. 1888, non *C. albida* Berk. & Curt. ex Cooke, Grevillea **12**: 78. 1884). Under the name *C. albida* Patouillard and Gaillard described a species on the larva of an unidentified insect from Atures, Venezuela. *C. albida* Berk. & Curt. had previously been published by Cooke for a fungus on crickets from Cuba. The latter appears to be the same as *C. albella* Massee which Petch (1931) has concluded is a Penicillium. The type of *C. albida* Pat. & Gaillard, No. 108, is in the Patouillard Collection of the Farlow Herbarium. The stromata which were described as white slightly yellowish are gray in the dried specimens. They are broken but apparently were clavate up to 20 mm long, with the upper perithecial portions 2–4 mm thick and the stipes 0.6–1 mm thick. The perithecia are narrowly ovoid attenuated above into narrow necks, 500–600 × 150–200 μ, with well differentiated brownish walls 15–20 μ thick. They are completely and somewhat obliquely embedded in a tissue consisting of closely interwoven hyphae without a differentiated cortex. The asci are cylindric 225–300 × 3–4 μ with a 2 μ thick cap. The ascospores are filiform and immature.

Cordyceps petchii nom. nov. (*Cordyceps ramosa* Petch British Myc. Soc. Trans. **21**: 42. 1937, non *C. ramosa* Teng, Sinensia **7**: 810. 1936). Petch described this species as on coleopterous larvae from collections in the Farlow Herbarium (FH6133 type and FH2626) collected by J. B. Rorer in Trinidad. Since Teng had previously used *C. ramosa* for a different species (see later discussion) it is necessary to rename the Trinidad species. The specimens cited by Petch have been studied. T. H. Hubbell of the Museum of Zoology has examined the specimens and has concluded that they are definitely on Lepidoptera larvae. The stromata are brownish gray, slender, 1 mm thick, up to 7 cm long and with up to 6 lateral branches which are up to 2 cm long (fig. 5). They consist of compact longitudinal parallel hyphae. The perithecia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are ovoid to ellipsoid (fig. 7), 300–420 × 156–280 μ, light brown to chestnut-brown with walls 30–40 μ thick. They appear to originate within the outer hyphae of the stromata but very early break through and become superficial and free (fig. 6). The asci are somewhat fusoid, 150–180 × 5–8 μ, with a 2.5–3 μ cap. The ascospores are filiform, up to 100 × 2 μ, multiseptate not breaking into fragments. This species is near to *C. acicularis* but is separated by its branched stromata.

Cordyceps erotyli Petch, British Myc. Soc. Trans. **21**: 40. 1937. This species was described by Petch from collections on *Erotylus* sp. (Coleoptera) from Trinidad. Collections 2622, 2625 type and 6120 made by Thaxter in Trinidad and 489 by Linder in British Guiana from the Farlow Herbarium have been seen. The stromata arise from adult beetles and are yellowish or whitish, clavate to subcapitate, slender, 4–15 mm long, 0.5–1 mm thick above with stipe 0.2–0.3 mm thick. The stipe and core of the upper perithecial portion consist of compact, longitudinal light brown hyphae. The perithecia are ovoid, 360–500 × 150–200 μ, light brown, with a 15–20 μ thick wall. They are embedded at right angles to the surface in a soft tissue consisting of interwoven hyphae without a differentiated cortex and the apices project due to the shrinkage of the tissue. The asci are cylindric, 150–300 × 3–4 μ with a slightly thickened cap, 1.5 μ. The ascospores are filiform, 1.5 μ thick. Part spores were not seen. Conidiophores occur on the mycelia up to 200 μ long. The phialides are narrowly ovoid, acuminate, 10–18 × 1.5–2 μ in terminal and intercalary groups of 2 or 3. The conidia are oblong 3–4.5 × 1.5 μ, hyaline. This species is very similar to *C. polyarthra* Möller which occurs on larvae of Lepidoptera (see Mains 1958a).

Cordyceps juruensis P. Henn. Hedwigia **43**: 248. 1904. There is a collection of this species in the Farlow Herbarium which appears to be part of the type. It is labeled "E. Ule. Herbarium Brasiliense No. 2817. *Cordiceps juruensis* P. Henn. n. sp. Auf Erdboden, Jurua, Marary. Amazonas. September 1900." The stromata are light grayish brown, clavate 4–8 cm long, with the upper perithecial portions 6–12 × 3–4 mm and the stipes 1.5–2 mm thick. The inner hyphae of the stipes and central cores of the perithecial portion are compact, longitudinal, somewhat interwoven, hyaline with the outer hyphae of the stipes dark brown. The perithecia are narrowly ovoid, 450–550 × 150–200 μ, with well differentiated brown walls, 20–25 μ thick. They are crowded and entirely embedded at right angles to the surface in a tissue

FIGS. 1–3, **Cordyceps parvula** sp. nov. FIG. 1, insect with stromata × 5. FIG. 2, stroma × 12. FIG. 3, perithecia × 50. FIG. 4, *Cordyceps trinidadensis* sp. nov. apex of stroma with perithecia × 40. FIGS. 5–7, *Cordyceps petchii*. FIG. 5, branched stroma × 1. FIG. 6, Portion of stroma showing superficial perithecia approx. × 8. FIG. 7, perithecia × 50. FIG. 8, *Cordyceps cicadicola* type, insect with stromata. FIG. 9, *Cordyceps nipponica*, Singer B2071, stroma with perithecial cushions, slightly enlarged. FIG. 10, *Cordyceps amazonica*, Singer B1408, stroma × 2. FIGS. 11 and 12, *Cordyceps flavella* (= *Claviceps flavella*) Singer B1160. FIG. 11, stromata × 2. FIG. 12, Head × 20.

consisting of loosely interwoven hyphae below and having a poorly defined cortex of brown pseudoparenchyma. The asci are cylindric, 250–350 × 6 μ with a 3–4 μ cap. The ascospores are filiform 1.5–2 μ thick; multiseptate with cells 2–5 μ long. The stromata bear conidiophores having heads of branches bearing spherical catenulate conidia, 2–2.5 μ in diameter as illustrated by Hennings. It is doubtful that this is the conidial stage. The host is unknown. Hennings noted similarities to *C. parasitica* (= *C. ophioglossoides*) which occurs on Elaphomyces sp. and to *C. olivaceo-virescens* on an unknown host. Petch (1933a) has concluded that the latter is *C. brasiliensis* which he states has oblique perithecia.

Cordyceps typhulaeformis Berk. & Curt. ex Cooke, Grevillea **12**: 78. 1884. *C. typhulaeformis* was described from a specimen in the Berkeley Herbarium (No. 8255) from Java. Massee (1895) has given a description and illustration of the type and Petch (1933a, 1942) has discussed the species and has concluded that *C. mitrata* Pat. *C. flavobrunnescens* P. Henn. and *C. coccinea* var. *subochracea* Penz. & Sacc. are the same. Among the specimens which he cites is a collection by Linder No. 2526 from Uganda in the Farlow Herbarium and one by Clemens No. 7793 F, from New Guinea formerly in the Missouri Botanic Garden now in the National Fungus Collections Washington, D. C. Both have been studied.

The Linder collection from Uganda consists of two clavate, brownish yellow to dark brown stromata, 15–20 mm long, 1 mm thick. The perithecia are ovoid, 300–400 × 200–220 μ, very closely crowded. The asci are cylindric 200–235 × 4 μ with a 2 μ cap. They are immature and mature ascospores were not seen.

The Clemens collection from New Guinea has a number of important differences. It is stated that the color was orange red when fresh. The stromata of the dried specimen have dark red stipes and ellipsoid heads with dark red perithecia in a soft light yellow tissue. The perithecia are ovoid 600–750 × 400–500 μ and the cylindric asci are 400–500 × 4 μ with 2–2.5 μ caps. The ascospores break into 1-celled segments, 2–4 × 1 μ.

There has been some question concerning the color of *C. typhulaeformis*. Cooke described it as carneo-rubra. Massee gives the type as flesh-color and Petch as brownish yellow or dark amber. Neither give measurements for the perithecia and asci. Massee gives the ascospores as 65–70 × 0.8 μ. The Linder specimen appears to agree with such information as is available concerning the species. In all except the shape of the stromata the Clemens collection appears to be *Cordyceps militaris*. Although that species usually has clavate stromata capitate variants have been noted.

Cordyceps ramosa Teng Sinensia **7**: 810. 1936. This species was described by Teng from Anhwei, China on a hypogeous fungus, Elaphomyces sp. The type, S. Q. Deng 701, is in National Fungus Collections, Washington, D. C. The stromata are broken but Teng describes and illustrates them as repeated

branched 3.5–4.5 cm long and 1.5–3 mm thick. They are cinnamon-brown and consist of compact longitudinal parallel or somewhat interwoven hyphae. The perithecia are ovoid, 350–420 × 250–300 μ, with a well differentiated wall 25–45 μ thick. There is a thin layer (50 μ) of interwoven hyphae between the bases of the perithecia but they are otherwise superficial and free. The asci are cylindric, 250–300 × 4–6 μ with a 1.5–2 μ cap. The filiform multiseptate ascospores are 1–1.5 μ thick with cells 1.5–3 μ long.

This is a very unusual species for the host. All the other species of Cordyceps parasitic on Elaphomyces have simple clavate or capitate stromata with the perithecia completely embedded and form a very closely related group (see Mains 1957) from which this species is markedly different.

Cordyceps grylli Teng Sinensia 7: 811. 1936. This species was described by Teng from Hainan, China on adults of Gryllidae (Orthoptera). The type specimen (Deng 3243) is in the National Fungus Collections, Washington, D. C. The stromata are broken. They are described as clavate with obtuse apices, yellow when fresh becoming grayish, with the upper perithecial portion 2–3 mm thick and the stipe 1–2 mm thick. The stromata consist of compact longitudinal parallel or somewhat interwoven brown hyphae. The perithecia are ovoid 400–700 × 300–350 μ, light brown or chestnut-brown, with walls 25–30 μ thick. They are partly embedded (up to one-half) in a layer consisting of loosely interwoven hyaline hyphae or are superficial and free. The asci are cylindric, 300–400 × 4 μ. The filiform spores break into 1-celled fragments 4–5 × 1 μ. It appears to be distinct from other species which have been described on Orthoptera.

Cordyceps cicadicola Teng, Sinensia 6: 191. 1935. This species was described by Teng from Hainan, China on adult Cicadidae. The type specimen (Deng 6179) is in the National Fungus Collections, Washington, D. C. The stromata are caespitose (fig. 8), very dark olivaceous brown, narrowly clavate with acute apices, 10–25 mm long, 1–2 mm thick above with stipes 0.5–1 mm thick. Teng gives the color as isabella when fresh. The stipe and central core of the upper perithecial portion consists of compact longitudinal somewhat interwoven brownish hyphae. The perithecia are ovoid to flaskshaped, 500–550 × 250–300 μ with thin 15 μ dark brown walls. They are obliquely embedded except for the slightly projecting apices in a tissue consisting of loosely, interwoven brownish hyphae below and very densely interwoven dark brown hyphae above. The asci are cylindric 350–400 × 4 μ with 1.5–2 μ caps. The ascospores are filiform, 1 μ thick, with cells 5–6.5 μ long according to Teng. From the description given by Kobayasi (1941) this appears to be *Cordyceps owariensis* Y. Kob.

Cordyceps arbuscula Teng, Sinensia 7: 812. 1936. This species was described by Teng from Hainan, China on larvae of beetles (Scarabaeidae). The type (Deng 3480) is in the National Fungus Collections, Washington, D. C. Although the stromata are broken they evidently were long (5–10 cm

according to Teng), slender, 1 mm thick, cylindric, much branched once or twice dichotomously as illustrated by Teng. The perithecia are ovoid, 425–500 × 225–300 μ, crowded, obliquely embedded with only the apices projecting in a tissue having closely interwoven hyphae below and a cortex of compact, parallel, longitudinal, brown hyphae. The asci are cylindric 200–300 × 4 μ with the walls only slightly thickened at the apices. The ascospores are filiform and immature.

Teng states that *C. arbuscula* appears to be close to *C. polyarthra* Möller. However, the latter has short, clavate stromata with the perithecia embedded at right angles to the surface in a soft stroma of interwoven hyphae without a cortex. The cortex of *C. arbuscula* is very usual. It is similar to that of *C. stylophora* (see Mains 1958a).

Cordyceps barnesii Thwaites ex Berk. & Br. Jour. Linn. Soc. **14**: 110. 1875. Teng (1935) reported this species from Hainan, China on larvae of beetles, Lamellicornia (Coleoptera). The specimen cited, Deng 3372, is in the National Fungus Collections, Washington, D. C. The stromata are 6–7 cm long. The upper perithecial portions are cylindric 10–15 mm long, 1–3 mm thick, dark brown, pale orange yellow when fresh according to Teng The stipes are 1–2 mm thick, dark brown and tomentose at the base. The stipes and central cylinder of the perithecial portion consist of longitudinal compact parallel or somewhat interwoven brownish hyphae. The perithecia are narrowly ovoid, 350–400 × 130–200 μ, with brown walls, 25–30 μ thick. They are entirely embedded and very closely crowded in a layer continuous over the apices consisting of loosely interwoven hyphae below and with a cortex of brown pseudoparenchyma between the necks of the perithecia. Asci were not seen apparently having disintegrated. The 1-celled part-spores are unusually long, 30–50 × 2 μ.

Massee (1895) and Petch (1924) have described and illustrated *C. barnesii* from the type and other collections from Ceylon. Both state that the stromata "usually" have acute sterile apices. Petch (1934) has concluded that *C. obtusa* Penz. & Sacc. differs from *C. barnesii* in having the "head continuous over the apex." The Deng specimens agree very well with the description and illustration of *C. obtusa* as given by Penzig and Saccardo (1904) except that they illustrate ascospores with short cells. However. Petch (1924) has stated that the part-spores of *C. barnesii* are variable being 30–40 × 2 μ in some asci and 9–12 × 2 μ in others in the Thwaites' specimens and others. It seems probable that *C. barnesii* and *C. obtusa* are conspecific. Petch (1934) has also concluded that *C. atrobrunnea* Penz. & Sacc. and *C. fleischeri* Penz. & Sacc. are the same.

Cordyceps oxycephala Penz. & Sacc. Icones Fung. Javan. p. 55, 1904. Teng (1935) has reported *C. oxycephala* on wasps (Vespidae, Hymenoptera) from Hainan, China, citing three collections, Deng. 3694, 3845 and 4386, which are in National Fungus Collections, Washington, D. C. The ochraceous

stromata are up to 6 cm long, capitate with cylindric heads 7–5 mm long and 0.5–1 mm thick, having short acute sterile apices and with stipes 0.2–0.3 mm thick. The stipe and central core of the head consist of compact, longitudinal, parallel or somewhat interwoven hyphae. The perithecia are conoid, 800–900 × 170–210 μ, with brown walls 15–20 μ thick. They are obliquely embedded in a tissue consisting of loosely interwoven hyaline hyphae below with a cortex of compact parallel brown hyphae. The asci are uncertain. The part-spores are somewhat fusoid, 8–10 × 1.5 μ.

It is very doubtful whether this species is distinct from *C. sphecocephala*, also on wasps. Deng distinguishes it from the latter by subcylindric head, acute apex and oblique perithecia. However, *C. sphecocephala* has oblique perithecia and the shape of the head is not significantly different. Although *C. sphecocephala* has rounded or obtuse apices it seems questionable whether this is sufficient to justify a specific separation. Petch (1933a) has concluded that *C. oxycephala, C. gentilis* (Ces.) Sacc., *C. lachnopoda* Penz. & Sacc., and *C. thrysoides* Möller are all *C. sphecocephala*.

Cordyceps nutans Pat. Bul. Soc. Myc. France 3: 127. 1887. This species was described by Patouillard from a specimen on a Hemiptera received from Japan. The type is in the Patouillard Collection of the Farlow Herbarium. The stromata are bicolored with the head and upper part of the stipe yellowish and the lower part of the stipe black. The heads are narrowly fusoid. The perithecia are conoid, 800–950 × 200–300 μ, with a brownish wall 15–20 μ thick, entirely obliquely embedded in a tissue consisting of hyaline interwoven hyphae with a cortex of brownish pseudoparenchyma having an ectal palisade-like layer of hyaline cells. The asci are 4–6 μ thick up to 400 μ long and the part spores hyaline, cylindric, 8–10 × 1.5 μ. This appears to be a common species in Japan (see Kobayasi 1941).

Two specimens from China, on Hemiptera in National Fungus Collections, Teng 1206 from Chekiang and S. Q. Deng 363 from Anhwei (see Teng 1934) are similar except that the perithecia are somewhat smaller, 650–700 × 150–200 μ. A specimen (M1109) collected by Rolf Singer on Edessa sp. (Pentatomidae) Frontera, Misiones, Argentina (MICH) has a stroma 7.5 cm long with an oblong head, 8 × 2 mm with an acute apex and with two short black sterile branches from the upper part. The head and upper part of the stipe is yellowish (red when fresh) and the lower part of stipe black. The perithecia are up to 1100 × 300 μ, the asci 500–650 × 6–7 μ with a 6 μ thick cap and part spores 8–10 × 1.5–2 μ.

Petch (1939) has reported the species from New Guinea and Moureau (1949) from Belgian Congo. Except for the bicolored stromata it is very similar to *C. tricentrus* also described on Hemiptera from Japan. Similar species having bicolored stromata have been described on ants (*C. australis, C. bicephala*) and beetles (*C. curculionum*) and Moureau has concluded that they are varieties of *C. bicephala*.

Cordyceps submilitaris P. Henn. Hedwigia **36**: 222. 1897. Teng (1934) reported this from Kaingsu, China on larvae of Lepidoptera and the specimen cited (Teng 1201) is in the National Fungus Collections, Washington, D. C. The stromata are clavate, simple or furcate, 3–9 cm long, the upper perithecial portions 2–6 mm thick, the stipes 1–4 mm thick, yellowish brown, reddish orange when fresh according to Teng. They are attached directly to the host as illustrated by Teng. The stipes and central core of the upper perithecial portion consist of longitudinal, compact somewhat interwoven brown hyphae. The perithecia are ovoid or flask-shaped, 500–700 × 300–400, obliquely embedded except for the projecting apices in a tissue consisting of compactly interwoven hyphae without a differentiated cortex. The asci are cylindric, 350–450 × 4 μ with a 2 μ cap. The ascospores are immature.

C. submilitaris was described by Hennings as on sphinx caterpillars (Lepidoptera). The collector, A. Möller (1901), has stated that the species occurred on beetle larvae (Coleoptera). *C. submilitaris* is a synonymn of *C. martialis* Speg. which is fairly common in the American Tropics on large coleopterous larvae. It has orange to cinnabar stromata usually attached by orange or red rhizomorphs to larvae covered by a red mycelium. The color is retained in dried specimens. The Teng specimens differs principally in being directly attached to lepidopterous larvae without a mycelial covering and drying to a yellowish brown color. It may be *C. cinnabarina* Petch from Madagascar which Petch (1933b) has stated is very similar to *C. submilitaris*.

Cordyceps nipponica Y. Kobayasi Bul. Biogeog. Soc. Jap. **9**: 151. 1939. *C. nipponica* as described by Kobayasi (1941) is on *Graptopsaltria nigrofuscata* (Cicadidae, Hemiptera) from Japan. It has been reported (Mains 1958b) from Brazil for a specimen in the Lloyd Herbarium (BPI). It is therefore very interesting to have a second specimen from South America. This (B2071) was received from R. Singer on Edessa sp. (Pentatomidae, Hemiptera) from Guayaramerin, Vaca Diez, Beni, Bolivia (MICH). The single stroma is 5.5 cm long, furfuraceous, terete, 1–1.5 mm thick, deep yellow when fresh, light yellowish brown dried (fig. 9). The perithecia are vertically embedded in two cushions, one laterally partly surrounding the stroma and the other terminating a short branch. There are also terminal and subterminal immature cushions. The perithecia are ovoid, 750–850 × 300–350 μ with brown walls 25–30 μ thick and entirely embedded in a tissue consisting of loosely interwoven hyaline hyphae with a differentiated cortex of brownish pseudoparenchyma 55 μ thick. The asci are cylindric, 500–600 × 4 μ with a 2 μ cap and the part spores are cylindric, 2–3 × 1 μ. The host of this specimen is not only in a different family from those previously reported but also in a different suborder.

Cordyceps amazonica P. Henn. Hedwigia **43**: 246. 1904. Hennings described *C. amazonica* from a specimen on Locusta sp. (Orthoptera), from

Brazil. Lloyd has reported it from Brazil but the specimen in the Lloyd Herbarium (BPI) is *C. nipponica* (Mains 1958b). It has also been reported (Mains 1940, 1958a) on cockroaches from British Honduras.

A specimen, B1408 (MICH), on a grasshopper (Orthoptera) has been received from R. Singer collected at Rio Yariza, Nor-Yungas La Paz, Bolivia. It has a single capitate stroma, 2 cm long, fig. 10. The head is brownish red, globoid, 35 mm in diameter. The stipe is reddish to yellowish, 1 mm thick. The perithecia are narrowly ovoid, 650–850 × 150–200 μ, with 15–20 μ thick walls and are entirely embedded at right angles to the surface of the head in a tissue consisting of loosely to closely interwoven hyphae below with a 75–120 μ thick cortex of brown pseudoparenchyma and a 35–40 μ thick. palisade-like ectal layer of multiseptate hyaline hyphae. The asci are cylindric, 450–550 × 4 μ with a 4 μ thick cap. The ascospores are filiform and break into cylindric, 6–8 × 1.5 μ part-spores. The asci of this specimen are much longer than the measurements given by Hennings and those of the British Honduras specimen. It is otherwise very similar.

Cordyceps australis (Speg.) Sacc. Syll. Fung. **2**: 571. 1883. This species has previously been discussed (Mains 1949). Three additional specimens have been studied. Two (Nos. M1079a, M1175) were received from R. Singer on ants from Frontera, Misiones, Argentina. They have bicolored stromata and ovoid heads and agree well with the description which has been given for the species. The third specimen occurred among the unidentified specimens in the National Fungus Collections, Washington, D. C. (BPI). It was collected on an "Azulu" ant, Tingo Mario, Peru, and was sent by J. B. Carpenter. It is of special interest since the head of the stroma is cylindric. It has a yellow cylindric head 6 × 1.2 mm and a stipe, 17 × 0.2 mm, which is black below and concolorous with the head above. The perithecia are conoid, 650–750 × 200–240 μ and are embedded obliquely to the surface. The asci are 450 × 4–6 μ. It therefore is apparently a variant of *C. australis*.

Petch (1933a) has concluded that *C. proliferans* and *C. huberiana*, which were described by Hennings (1904, 1908) as having bicolored stromata, differ from *C. bicephala* (= *C. australis*) in that they have cylindric heads and probably are variants. Hennings describes and illustrates the perithecia as ovoid, 150–180 × 4–5 μ embedded at right angles to the surface and the asci as cylindric 150–180 × 4–5 μ. Unfortunately, although Petch states that he saw the type of *C. huberiana* he does not give data concerning perithecia and asci. It is possible that Hennings reached erroneous conclusions through a study of cross sections of the heads in which the oblique perithecia would have been cut across. It seems best to consider both as doubtful species.

Cordyceps curculionum (Tul.) Sacc. Michelia **1**: 320. 1879. Three specimens of this species were received from R. Singer from South America on beetles (MICH). No. T1279 from Las Lenguas, Tucumán, Argentina and No. B1552 on Staphylinidae, Carmen Pampa, Nor-Yungas, Las Paz, Bolivia.

have slender, 0.2 mm thick, bicolored stroma with ovoid yellow or yellowish brown heads (deep rose-pink when fresh) 1.5×1.5 mm and black stipes. They agree well with the description of the species which has been given elsewhere (Mains 1958a). Another collection, B2085, on a large adult beetle from Guayarameren, Vaca Diez, Beni, Bolivia differs in having a more robust stroma with a stipe 1 mm thick and a cylindric head 11×1.5 mm. The shape of the head is more like that which occurs in *C. nutans* with which it is very closely related.

Cordyceps sphecocephala (Berk.) Sacc. Michelia **1**: 321. 1879. A specimen of this species (T1424) has been received from R. Singer on a wasp from Rio Piedras, Salta, Argentina (MICH). It has a single slender, yellowish brown stroma approximately 5 cm long with a yellowish fusoid head, 3×1.5 mm. It has conoid perithecia, $900–1000 \times 200–250$ μ, entirely embedded obliquely to the surface in a tissue of loosely interwoven hyaline hyphae with a cortex of pseudoparenchyma having an ectal layer of hyaline oblong cells. The asci are cylindric $500–600 \times 4–6$ μ with 4–5 μ caps. The part-spores are fusoid, $10–12 \times 1.5$ μ.

Two specimens (BPI) have been seen from China which were reported by Teng (1934). The one (1207) collected by S. C. Teng on Vespidae is an immature specimen. The other (S. C. Teng 1205) is given as on Cercopidae (Hemiptera). Unfortunately only stipes remain. This specimen was first determined by Teng as *C. tricentri* but later he decided that the two were conspecific. They differ very little morphologically and are separated mostly by their hosts. If they are treated conspecifically it would be desirable to recognize them as varieties as Moureau has done for *C. bicephala*, *C. nutans*, and *C. curculionum* under *C. bicephala* and with which they are very closely related. The relationships have been discussed elsewhere (Mains 1958a).

Cordyceps gracilis Dur. & Mont. Fl. Algérie Cryp. **1**: 449. 1846. Four specimens of this species were received from R. Singer from Argentina and Bolivia. Three, T1142 from Tucumán, Argentina, T2089 from Sierra San Javier, Argentina and B1850 from Vaca Diez, Beni, Bolivia have unidentified hosts. The fourth, B1050, on fragments of Elateridae (Coleoptera) was collected in Nor-Yungas, La Paz, Bolivia. A specimen from Brazil on coleopterous larvae also occurs in the Lloyd Collection in National Fungus Collections, Washington, D. C. The species was described from larvae of Lepidoptera but occurs on both Lepidoptera and Coleoptera in North America as has been discussed elsewhere (Mains 1958a).

Cordyceps dipterigena Berk. & Br. Jour. Linn. Soc. **14**: 111. 1875. Two specimens (B979, B1423) on flies (Diptera) were received from R. Singer collected in La Paz, Bolivia (MICH). They agree with the description which has been given for the species for North America (Mains 1958a). *C. dipterigena* has been previously reported for Trinidad, British Guiana, Surinam and Brazil.

Cordyceps flavella Berk. & Curt. Jour. Linn. Soc. **10**: 375. 1869. (= *Claviceps flavella* Petch, Brit. Myc. Soc. Trans. **18**: 49. 1933). *Cordyceps flavella* was described from a collection of Charles Wright (519) from Cuba and it is stated that it apparently was growing on some Sclerotium. There is a specimen in the Curtis Collection of the Farlow Herbarium which apparently is a portion of the type collection. It consists of four slender capitate stromata, 10–13 mm long with stipes 0.2 mm thick and spherical heads, 0.5–0.7 mm in diameter. The stipe consists of longitudinal parallel hyphae which diverge and become interwoven in the head. The heads are brown slightly roughened by the ostioles and the stipes light brown somewhat translucent. The heads extend slightly downward, over and free from the stipe forming a slight collar. The perithecia are ovoid, 200–225 × 90–100 μ, entirely embedded at right angles to the surface in a tissue consisting of interwoven hyphae without a differentiated cortex. The asci are cylindric 100 × 2–2.5 μ with a 1 μ thick cap. They are immature and the ascospores are uncertain. The stromata arise from small black sclerotia in the glumes of some gramineous (?) plant.

A collection of this species has been received from R. Singer, B1160, from Coroico, Nor-Yungas, La Paz, Bolivia (MICH). The capitate stromata are 8–20 mm long, one or two from black irregular sclerotia (fig. 11). The heads are subgloboid to oblong, 1–1.5 × 0.7–1 mm, light yellowish brown, projecting downward to form a small collar free from the stipe (fig. 12). The stipes are lighter in color, slender 0.2–0.3 mm thick. The perithecia are ovoid 280–320 × 150–200 μ with well defined brownish walls, 10–15 μ thick. They are embedded except for the apices in a tissue consisting of loosely interwoven hyaline hyphae with a cortex consisting of brownish pseudoparenchyma. The asci are cylindric, 150–175 × 2–2.5 μ and have 1 μ thick caps. The ascospores are filiform, 0.5 μ thick.

Petch (1933a) transferred the species to Claviceps and concluded that *Claviceps balansoides* described by Möller (1901) on spikelets of Panicum from Brazil is conspecific. Möller (1c fig. 73) gives good illustrations of the species. Diehl (1950) also states that the type of *Claviceps pallida* Pat. in the Patouillard Herbarium in the Farlow Herbarium which was collected by Duss in Guadeloupe is *Claviceps flavella*. Lloyd reported the species from Brazil but as has been stated elsewhere (Mains 1958b) the specimen, LH 41264 (BPI), is *Cordyceps gracilis*.

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A METHOD TO DETERMINE THE LENGTH OF INDIVIDUAL ROOTS[1]

HOWARD J. DITTMER

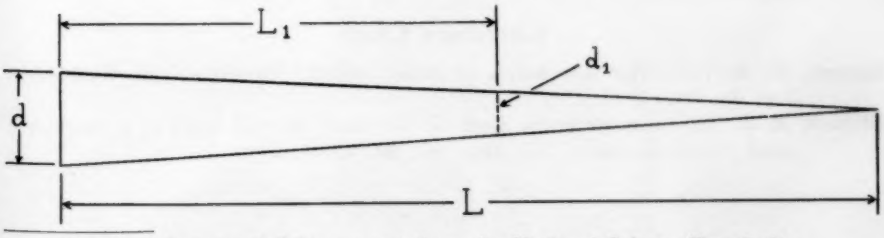
Information concerning the characteristics of root systems is important in determining the absorptive and conductive capacities of a plant as well as the variability of roots in depth of penetration, lateral spread, and the number and size of main and branch roots. Difficulties encountered in studies of this nature have been noted by a number of investigators. Helmers and co-workers (1955) observed variations in the roots of chaparral plants and pointed out the problems in making a complete study of root systems. Earlier studies by Cannon (1911) of the root systems of desert plants and those of Weaver (1925) of field plants described methods used in studying the major roots of many plants. Direct counts and measurements of complete root systems were made by Pavylechenko (1937) and Dittmer (1937). Kalela (1954) studied the root potential of pine by counting the number of root tips produced by a single plant.

In the present paper, the writer proposes a method for calculating the probable depth of vertical penetration and lateral extension obtained by individual roots. It is known that certain plants ultimately grow into the water table even though this water may be thirty or forty feet beneath the soil surface. By the method described here a very close approximation can be made for the total length of an individual root and conversely if we know the root habits of a certain plant, we may also judge the approximate depth of the water table itself.

If one treats the root as an elongated cone and uses the following formula he can ascertain quite accurately the total length of the root.

$$L = \frac{L_1 \cdot d}{d - d_1}$$

d = the diameter of the root at the base of the plant.
d_1 = the diameter at the distal broken end of the root.
L_1 = the actual length of the recovered portion of the root.
L = the total projected length of the root.



[1] This work is supported by a grant from the National Science Foundation.

Calipers graduated to tenths of a millimeter are used in measuring the diameters of the largest roots, and an ocular micrometer in a compound microscope is used in measuring the diameters of those less than 1 millimeter in diameter. Care should be taken to measure the root away from places of secondary root origin where the diameter is usually abnormally large. Gnarled and twisted roots must also be avoided but where the growth of the root is uniform and where the measurements are carefully taken, the method has a high degree of accuracy. Fresh living roots should be measured wherever possible, since many roots dry irregularly and may contribute to an erroneous calculation. In the roots measured thus far and checked against actual length the error has been less than 10 per cent.

Scoparius dalea has a widespread root system with relatively little depth but very extensive radial growth from the base of the plant. One root had a basal diameter of 11.2 mm. and 91.4 cm. from the base it measured 7.0 mm. The calculated total length for this root is 243.8 cm. and its actual length was 227.8 cm. Cannon (1911) described a short root of *Datura*, which tapered rapidly, as under 10 cm. in length; at the crown the root was 4.5 mm. in diameter and 8 cm. from the crown it measured 0.5 mm. in diameter. The calculated total length is 9.0 cm. or within the 10 percent error allowed by this method.

The long tapering roots of *Opuntia arborescens* are also ideally suited for this method. Normally the numerous roots of its fibrous system are concentrated in the upper two feet of soil but in many plants long roots develop laterally and trail out a good many feet from the base of the plant. One such root, which never was more than 4 inches beneath the surface except for its laterals, measured 13 mm. in diameter at its basal end and 4 mm. at its distal end. The total length of this broken piece was 338 cm. Its calculated total length was 488 cm. and its actual length, when the remainder was recovered, was 458 cm.

Although only major roots have been described, the method is equally applicable to secondary and tertiary roots arising from the main roots of the plant. Monocotyledonous roots can be studied in the same way although in almost all cases it is necessary to measure the diameters by means of an ocular micrometer in a microscope.

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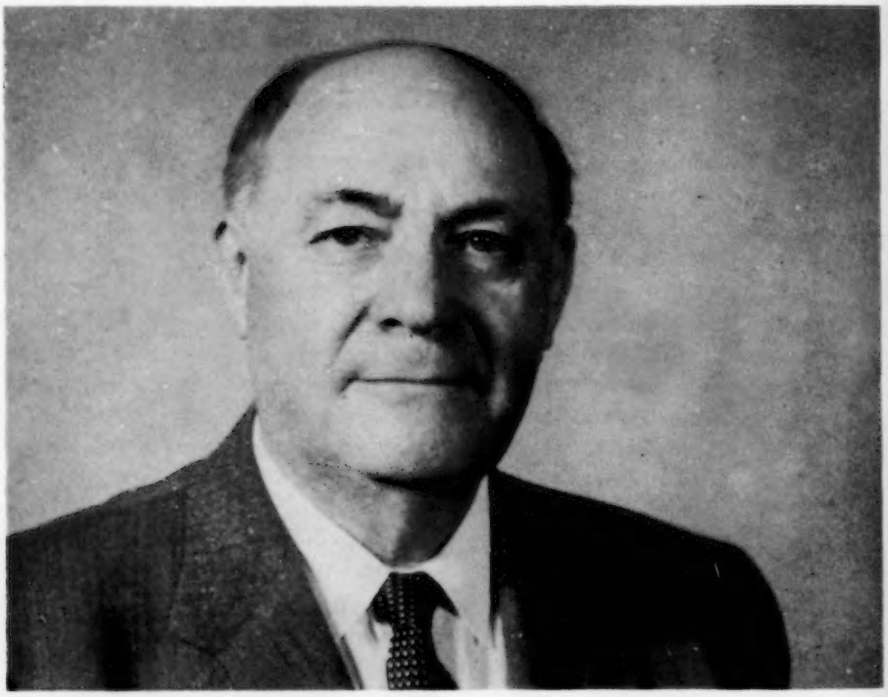
TORREYA

Percy W. Zimmerman

LELA V. BARTON

The Torrey Botanical Club shares with Boyce Thompson Institute for Plant Research, and indeed with the botanical world at large, the sense of loss in the death of Dr. Percy W. Zimmerman on August 14, 1958 at Wenatchee, Washington. Characteristic of his sustained vigor and interest in his chosen field, he was representing his institute in an inspection of the effect of air pollutants on fruit trees when he was stricken with an embolism following an operation.

Dr. Zimmerman was born at Manito, Illinois, February 23, 1884. He attended Eastern Illinois State Normal College from 1907 to 1910. From 1910 to 1913, he was the superintendent of schools at Westville, Ill. His B.S., M.S. and Ph.D. degrees were



Percy W. Zimmerman February 23, 1884–August 14, 1958.

all obtained at the University of Chicago. Immediately following the earning of his M.S. degree he was an assistant in the Botany Department of the University. From 1916 to 1925 he was at the University of Maryland, serving in the capacities of Associate Professor of Botany, Acting Dean of the Division of Plant Industry, and Professor of Botany and Dean of the College of Agriculture. From 1925 to 1927, part of his time was spent at Boyce Thompson Institute for Plant Research and part at the University of Maryland, where he continued as Professor and Associate Dean. From 1927 to the time of his death, he held the position of plant physiologist at Boyce Thompson Institute.

Dr. Zimmerman had a wide interest in and an unfailing enthusiasm for the science of Botany. He was, perhaps, most concerned with the effects of growth regulating substances and air pollution on plant growth. It was in these fields that he attained international recognition. With his associate, Dr. A. E. Hitchcock, he helped to establish the importance of plant hormones and growth regulants, and shared in the 1935 Annual Award of the American Association for the Advancement of Science for pioneer work in this field. The practical importance of this basic research was recognized by the American Society for Horticultural Science which gave its Vaughn Award for the experiments with substituted phenoxy acids and other growth regulants which were effective for increasing fruit set and inducing seedless fruit. The first work on the weed-killer, 2,4-D, was carried out in Dr. Zimmerman's laboratory, with the first published report in 1942. One has only to note the many uses and the volume of sales of this product to realize the significance to the world at large of such a discovery. Experiments carried out under Dr. Zimmerman's direction established the control of the water hyacinth in Louisiana by the use of 2,4-D, a benefit which has now been extended to the vital waterways of Africa which were being choked by this plant.

With his associate, he also received the A. Cressy Morrison Award of The New York Academy of Sciences in recognition of work relating to the initiation and stimulation of roots from exposure of plants to carbon monoxide gas (the first use of a known chemical for inducing the formation of a plant organ).

Dr. Zimmerman was interested not only in the growth of plants but also in the growing of them. This was, perhaps, most evident in his attention to holly and to camellias. The increasing popularity of garden camellias in regions with rather severe winters has been due in part to his demonstration of their hardiness. He also produced new camellia hybrids which were successfully established in his garden and in the gardens of his friends.

More than 200 published titles list the interests and accomplishments of Dr. Zimmerman. Most of these have co-authors, for this man conducted and published research as one of a partnership or a team. His contacts and keen awareness of problems to be solved, his enthusiastic approach, and his guidance of a team in the solution of the problem at hand were among his outstanding characteristics.

The wealth of Dr. Zimmerman's interests and activities is represented by the societies of which he was an active member. These included the American Society for Horticultural Science, Plant Physiology Section of the Botanical Society of America, The Torrey Botanical Club, American Association for the Advancement of Science, American Chemical Society, Westchester Chemical Society, American Horticulture Council, Weed Society of America, Florida State Horticultural Society, Air Pollution Control Association, Camellia Society of the Potomac Valley, Sigma Xi, Alpha Zeta and Phi Kappa Phi.

Dr. Zimmerman served Boyce Thompson Institute long and faithfully, but he was also noted for his community service. In the latter capacity he has been associated with the Boy Scouts, the American Red Cross, the Salvation Army, Board of St. John's Riverside Hospital, and numerous societies and clubs of Yonkers, N. Y. At the national level, Dr. Zimmerman was asked in 1950 to organize an Agriculture Panel for a U. S. Technical Conference on Air Pollution called by former President, Harry S. Truman. Later, he was placed on a steering committee to determine the course of further study of this problem and to make recommendations to implement the findings.

The Torrey Botanical Club has special reason to regret his passing, for he contributed much to the club throughout the years of his residence in the New York area. He has lectured to the club on many occasions, the first of which was on April 17, 1929, when he spoke on "Special Phases of Plant Propagation". Through the years since that time his lectures to the club have been on such topics as "How Mercury Compounds Applied to Soil Contaminate the Air and Injure Plants", "Effect of Chlorinated Water on Land Plants, Aquatic Plants and Gold Fish", "A General Discussion of Growth Substances", etc. He has also participated in exhibits staged by the club. He served on the Council of the club continuously from 1939 to 1948, and was president in 1946. He has also been a member of the Program and Local Flora Committees. In addition to these

offices he has represented the club on the Council of the AAAS and on the Board of Managers of The New York Botanical Garden. He was a member of the club for 29 years, having been elected to membership in October, 1928.

In the death of Dr. Percy W. Zimmerman, Botany has lost a staunch advocate, and many people and causes have lost a good friend.

FIELD TRIP REPORTS

August 2–3, 1958. Litchfield and Norfolk, Conn. Several areas of botanical interest on the property of the White Memorial Foundation including Catlin Woods, an uncut mature mixed woodlands, were visited on the first day of this trip. A number of midsummer flowers such as *Habenaria psycodes, H. Lacera, Lobelia cardinalis,* and *Chimaphila maculata* were found in bloom. There were also an unusual number of *Monotropa uniflora, M. Hypopitys,* a variety of mushrooms, and berries of various sorts to be seen, apparently due to the wet spring and early summer. The plants which were particularly heavy with fruit included *Lonicera tacarica* (with both red and orange berries), *Viburnum alnifolium, V. dentatum, V. opulus, V. lentago, Cornus amomum, C. racemosa, Corylus americana, C. cornuta,* and *Rhus vernix.* On the second day of the trip a visit was made to Beckley Bog, a black spruce-larch-sphagnum bog in Norfolk, Conn. A number of ericaceous plants were seen at the bog including *Ledum groenlandicum, Kalmia polifolia, K. angustifolia, Andromeda glaucophylla, Chamaedaphne calyculata, Vaccinium oxycoccos* and a high-bush blueberry which may be *V. caesariense. Nemopanthus mucronata* in fruit, *Myrica gale subglabra, Drosera rotundifolia, D. intermedia, Sarracenia purpurea, Utricularia cornuta, Habenaria blethariglottis, H. clavellata, Rynchospora alba* f. *laeviseta,* and *Lycopodium inundatum* were also seen in or around the bog. *Attendance* 20. Leader, Gordon Loery.

August 10. Charleston, Staten Island, N. Y. The woodland near the pond on Sharrott road had been burned over and was getting a fresh start with poison ivy, catbrier, sassafras, and grey birch. Most of the trees had been killed. A large stand of buttonbush was in bloom in the pond and these shrubs were attracting many black swallowtails and other butterflies. *Scleroderma vulgare, Cantharellus auranticus* and a *Russula* were found in the woodland. In more open spaces were *Solidago juncea, Eupatorium album, E. purpureum, E. hyssopifolium, Asclepias tuberosa* in bloom, and *A. syriaca* with ripening seed pods. In the afternoon we visited the cemetery of the African Church. It was badly neglected and the trees, shrubs, and herbs that grew there were suffering from poor soil. Sassafras trees are inclined to overrun the area and we found little of interest. The ponds along Clay Pit road, which had been dug out in an effort to utilize the clay during the early part of the century, had gradually filled in and were overgrown with swampland vegetation, *Phragmites,* cattails, and tearthumb being conspicuous. Attendance 7. Leader, Mathilda Weingartner.

September 7. Jamaica Bay Sanctuary, Brooklyn, N. Y. The Jamaica Bay Wildlife Refuge is located on the border of King's and Queen's Counties, on Long Island. Two tidal basins have been diked and the impounded waters are known as the East and West Ponds. At present these ponds are about fourteen percent saline and encroachments of fresh marsh plants are evident. The adjacent tidal flats and saltmarsh, together with the brackish ponds, offer excellent feeding conditions for a variety of shorebirds and waterfowl.

We had able assistance from botanists and birders and were able to cover both ponds and the nearby saltmarsh areas. Mr. Joseph Monachino was invaluable as an assistant. He not only worked wonders with the plants of the area (see attached report) but he also found an injured tree swallow, which we took along on our trip. This bird was remarkably tame and fearless and the members were kept busy finding insects to feed it! Tiger beetles, assorted moths and butterflies, puree of small grasshoppers and crickets, damsel flies, etc. were eagerly accepted. Most of us had a spell of toting the critter around all day. We finally caught up with the stanctuary manager Mr. Herb Johnson, who took the bird home for further care.

Fine views were had of snowy and American egrets, (40) herons and black skimmers (250). A family of ruddy ducks, (10 young, 2 adults) were observed. A juvenile black duck, suffering from an advanced case of botulism, was taken to a nearby clean pond in hopes that it would recover. At any rate it was advisable to remove it from the main pond as this is a deadly disease of waterfowl.

We had a wonderful day and the attendance of thirty shows the interest in this area. Leader, Edward J. Whelen.

Plant report. The two most colorful flowers seen on the Jamaica Bay Sanctuary trip are the purple gerardia, which displayed a mass of rose-purple along a walk showy enough to rival any cultivated flower border, and the golden aster or camphorweed. The two common names of the latter are also applied to *Chrysopsis* and *Pluchea*, respectively. The camphoric golden aster looks more like *Chrysopsis* (not seen during the trip) and smells more like *Pluchea* (the marsh fleabane or camphorweed, which we did see), but specifically it is *Heterotheca subaxillaris*, an introduction from the South. It now grows abundantly in the area, and I have also seen it near Sheepshead Bay and in Marine Park in Brooklyn and on Staten Island. *Heterotheca* was first reported for Long Island (Idlewild Airport) in 1954 (Rhodora **56**: 182), although it had been seen in New York City since at least 1950. We examined four species of *Eupatorium* (*E. dubium, E. hyssopifolium, E. perfoliatum, E. pilosum*); also *Solidago tenuifolia, Aster subulatus, Epilobium hirsutum*. The great hairy willow-herb is now frequent and locally abundant in the City area. Gleason gives its distribution as "Que. to Ill.", a one-dimensional range! There is a good stand of the subshrubby *Lechea maritima*. Rare as it once was, *Cycloloma atriplicifolium* is now very common in the City coastal regions. We learned that the hairy sea-blite, *Bassia hirsuta*, can be easily distinguished from *Sueada* by its minutely gray-villous calyx and young foliage. The species of *Cyperus* particularly noted are *C. filicinus, C. grayii* and *C. esculentus*. There are scattered bold clumps of *Carex silicea*, identified by its moniliform arching whitish spikes. Of the grasses, there is the acid-tasting *Triplasis purpurea; Digitaria sanguinalis*, with its purplish cast, lends color to the landscape; *Cenchrus pauciflorus* is a nuisance, but *Aristida tuberculosa* at this time is still safe to tread upon. Most interesting is the silver grass, *Corynephorus canescens*, which thickly besets the area with glaucous-green tufts. This species was first reported for North America by Eugene Bicknell who collected it on Long Island near Hempstead Reservoir in 1903, and 1905 found it in abundance in South Jamaica (Rhodora **16**: 81). Actually there are extant earlier specimens collected by Parker on ballast in Philadelphia in 1878. In 1936, I collected a specimen from Cross Bay Boulevard for the Local Herbarium of The New York Botanical Garden and I noted its abundance even then. What might account for its prolific generation? Has anyone found it seeding? I have not. There is a field observation I can offer as a result of the September 7 walk: At this late season most of the early flowers in the silver grass have been shed, only the glumes remaining. But straddled on the nodes of the culms I noticed occasional young tufts, bearing roots even while on its aerial perch, which sometimes detached at the slightest touch and dropped on the sand, perhaps thus to start new individuals. Can it be that the species is viviparous!

As to be expected, there are hardly any trees, except for the introduced Russian olive, *Elaeagnus angustifolia*, heavily bearing ivory faintly-yellowish and mealy-sweetish drupe-like fruits. There are seedlings about. They have oval velvety leaves thickly covered with stellate hairs composed of many fine rays, quite different from the indumentum of silvery peltate scales found on adult leaves.

I shall terminate my incomplete list of the plants observed on the September 7 walk by mention of the cottonweed, not before seen by me in the City, *Froelichia* grows in the sandy stretch adjacent to the Rockaway Railway. The several dozen plants seen all have simple stems. Those examined (voucher, Monachino 628) have the lateral wing-like crests on the calyx varying from irregularly erose to deeply toothed. If we wish to be technical, I can say that these crests, still somewhat membranous in our plants, are similar to those of Bush 6273 from Missouri, examined for the North America Flora, named *F. gracilis*. However, I am not sure that this character is trustworthy for distinguishing the species

from *F. floridana*. There are many specimens named *F. floridana* in the herbarium which have crests like those illustrated for *F. gracilis* in Gleason's New Illustrated Flora. The genus, I suspect, needs revision. *F. gracilis* has already been reported for New York State, Monroe and Putnam Counties (Rhodora **58**: 35–38. 1956).—Joseph Monachino.

September 14. Stony Brook, Rockland Co., N. Y. The Torrey Botanical Club was fortunate in having guest-leader Guy Nearing, one of the best all-around field botanists in the local range. He is author of THE LICHEN BOOK. I can testify that both the book and its author have been an immense inspiration to amateur lichenologists. The trip attendance and enthusiasm were tremendous. The help by Bill Rissanen and Dr. Elva Lawton, particularly with the mosses and liverworts, was much appreciated. J. Harry Lehr brought along copies of his AN ANNOTATED PRELIMINARY CATALOGUE OF THE VASCULAR FLORA OF ROCKLAND COUNTY, NEW YORK. Although lichens and fungi were our principal objective, we stopped to admire the porcelain-blue (so described by Fernald) *Gentiana clausa* and the feathery-slender wood horsetail, the branching form with the sesquipedalian name *Equisetum sylvaticum* var. *pauciramosum* f. *multiramosum*. The youngest member of our group, fifteen year old Dorothea Bedigian (accompanied by Elizabeth Hall) was induced for the first time in her life to touch the silky skin of a snake, the smooth green snake captured and identified by Jim McGrath. Such are the beginnings whereof herpetologists are made!

The star find of the day was an unearthly slate-blue colored polypore not recognized by anyone in the group. Specimens were taken by Dr. C. T. Rogerson, Mycologist of The New York Botanical Garden, who subsequently reported: "The blue-colored fungus collected on the Torrey trip, September 14, proves to be *Polyporus caeruleoporus* Peck. Overholts (1953) stated that it is a rare plant of which perhaps not a dozen collections are known in America. It has been recorded from Maine, Vermont, New York, Pennsylvania, North Carolina, New Brunswick, and Ontario. The North Carolina collections had been named *Polyporus holocyaneus* Atk. which is now considered to be a synonym. Murrill called it *Scutiger caeruleoporus* (PK) Murr." Most interesting to me was *Glonium stellatum*, a fungus that off-hand appeared as black-charred woods, but under the lense displayed a delicate tracery of ripples, tiny discoid thalli ornamented with fine forking ridges radiating from the center.

What flowering plants seen on the walk are species not listed in Lehr's Catalogue? I noted six: *Elymus riparius, Glyceria melicaria, Desmodium perplexum, Lechea villosa, Gratiola neglecta, Hieracium scabrum*. In addition, Jim McGrath collected a grass which appeared to be *Muhlenbergia tenuiflora;* but I did not examine it. As I'm not sure about the different elements in the "*Desmodium dellenii* complex", I sent the specimen to Bernice G. Schubert who provided the identification. Dr. Schubert wrote: "I agree that it is not very easy to distinguish between *D. perplexum* and *D. glabellum* and I hope sometime I will be able to clarify the key so that it will be more usable." This is a matter, like many others, in which local botanists can help! Attendance 35. Leader, Joseph Monachino.

September 21. Van Cortlandt Park, N. Y. I went to Van Courtlandt Park to meet group, but because of rain no one came. Leader, Jane Meyer.

September 28. Latourett Park, Staten Island, New York. Fall coloring was just beginning in the sweet gum trees, sour gum trees and some grasses. The fruit on the osage orange trees were not quite ripe. Hackberry trees were attracting robins and cardinals with their berries. Some of the gamma grass was still in bloom. Bayberries do not seem very abundant this year. Nuts were found under two kinds of hickory trees: *Carga alba* and *C. glabra* as well as the black walnut. Three eupatoriums were seen: *Eupatorium album, E. perfoliatum,* and *E. purpureum*. There was also a large stand of Indian pipe, which had put in an appearance after the heavy rain the night before the trip. Sumachs seen were: *Rhus glabra, R. vernix, R. hirsutus* and *R. copalina*. Bittersweet was not in fruit in this area, it possibly being a staminate plant. On a stand of persimmon there were several fruits, but no ripe one. In a wet depression we found a

stand of closed gentian and *Lycopodium adpressum*. Three kinds of Chokeberries lent their color to the landscape: *Pyrus melanocarpa, P. atro-purpurea,* and *P. arbutifolia.* There were several specimens of *Acer negundo* on a bluff. *Viburnum prunifolium, V. acerifolium* and *V. dentatum* were also in fruit, as were *Cornus amomum* and *C. paniculata.* New England Asters lent their lovely purple color in the bright sunshine. Attendance 7. Leader, Mathilde P. Weingartner.

October 12. Pelham Bay Park, Bronx, N. Y. C. The most gratifying thing about the trip to the leader was the young age level of the fourteen participants. It is good to have the old-timers come along to wisely guide us and to reminisce about the varied experiences of the past, but we also need youngsters who are the future of the Torrey Botanical Club. Also delightful to the leader—and this is a selfish matter—was his find of a giant fungus, *Polyporus frondosus.* Some five pounds of it was carted home by him and, as he writes this report, it is still furnishing a delectable garnishment to his evening meals. Its texture after parboiling is like a cock's comb. The species has been aptly called the cauliflower mushroom. The same was seen the previous month on the Stony Brook trip led by Guy Nearing. A portion of the Pelham specimen was checked for its specific identity by Dr. C. T. Rogerson, Mycologist of The New York Botanical Garden.

All professional botanists teaching amateurs are sometimes a little embarrassed in explaining the vagaries of technical nomenclature. There is a kind of synonymy—the *"sensu"* type of synonymy—which is especially difficult to put across. It was just this problem that was harped upon on the Pelham trip. The leader pointed to *Aster ericoides* (sensu latest manuals). "The plant was previously called *A. multiflorus,*" he explained, "the name *A. ericoides* being applied to this other quite different species growing nearby, now named *A. pilosus* var. *demotus.*" "Here is a grand colony of *Gerardia flava.* In the 7th Ed. Gray, which I have in my sidebag, this glabrous glaucous species is called *G. virginica,* a name now applied to the downy false foxglove." And so on and on. *Acalypha rhomboidea;* it was called *A. virginica,* a name now applied to another species. *Potentilla simplex;* a few years ago called *P. canadensis,* a name now applied to another closely related species. *Pycnanthemum tenuifolium;* still called *P. flexuosum* by Gleason in his New Britton and Brown (1952), but this name is applied to a southern species by Fernald in his 8th Ed. Gray (1950). *Euphorbia supina* and *E. maculata* (sensu Fernald); the latter name is still applied to the former species by Gleason, so that "*E. maculata* L." according to Fernald and the same name according to Gleason stand for two quite different spurges. *Oxalis stricta,* as agreed upon by both Gleason and Fernald but not as it is interpreted by the latest student of the genus, and not as it will be applied in a new manual now in preparation. Indeed, we saw two quite different species of yellow sorrel, which, by following different authorities, one can call by the very same binomial, "*O. stricta* L."! We spoke about other local flora plants cursed by a distressing synonymy. *Sisyrinchium angustifolium* (sensu Fernald 1950); Alexander in Gleason (1952) still calls the species *S. graminoides* and still accepts *S. angustifolia* in the sense of the 7th Ed. Gray. *Liatris novae-angliae,* called *L. borealis* by Fernald; we previously called it *L. scariosa,* but this name now refers to a species outside of our range. And so on; and mark you, we are trying to explain these intricacies to young students of flowers and trees, not to lawyers. How shall we extricate ourselves! Leader, Joseph Monachino.

October 18. Holly Tour, Central New Jersey. Three members appeared at Horticultural Farm No. 1 of the New Jersey Agricultural Experiment Station to enjoy the holly and songbirds. The weather was clear and brisk. Fruits were attractive on black alder, *Ilex verticillata* and *serrata,* its Asiatic complement. English and Perny hollies had begun to show bright color. Only a few varieties of American holly, such as "Griscom", "Farage" and "Old Harry Berry", were red. The inkberry and its Japanese counterpart, *I. crenata,* were berried. The Rutgers holly collection contains over 200 selections of American holly with numerous cultivars of English, Chinese and Japanese hollies. Leader, Robert B. Clark.

BOOK REVIEW

Les Charophycées de France et d'Europe Occidentale. By Robert Corillion. 499 pp., 64 charts, 35 pl., numerous text figures. Travaux Lab. Bot. Faculté des Sciences d'Angers, Fasc. 11 et 12. Année 1957. Imprimerie Bretonne, 38 Rue du Pré-Botté, 38, Rennes, France.

This work is another in an impressive series of regional floras on Characeae which have appeared in the last three decades. Like the preceding works, the author has expanded phytogeographic knowledge of the species. However, Corillion has especially expanded the treatment of ecology, and the reviewer feels that this is the author's most significant contribution. His analyses on the phytosociology of the group is of fundamental importance, and his discussion of the dynamic synecology of *Characeae* is new. A great deal of field experience has been concentrated into a number of revealing cross-sectional diagrams of natural habitats.

A second novel feature is the author's report of culture studies of various species of *Chara* grown in vitro with augmented alkalinity (200 mg. CaO/liter; pH 7.7). This was achieved by using a mildly calcareous substrate in the bottom of test tubes, and by using weakly acid water low in dissolved salts. Observations were continued for over a year with only addition of water. The Charads became empoverished and entered a state of suspension of growth. Under such conditions, abnormalities developed in a number of examples which the author interpreted as being identical to characters of other species. Thus, he offers this as an experimental means of revealing conspecificity. Of special interest was the empoverishment-induced variations of *Chara vulgaris* which produced (1) a decrease in number of corticated branchlet segments, (2) a separation of sexes on branchlet, with resulting change from conjoined to disjunct arrangement, and (3) a repression from two to one sex on a branchlet. In this way, he united *C. vulgaris, C. squamosa,* and *C. Rabenhorstii.* In another case, he united *C. contraria, C. denudata, C. dissoluta, C. jubata,* and *C. arrudensis.* This interpretation, though interesting, will meet with requests for further confirmation. Spore germination occurred at 15° C., and commonly began within 20 days.

In the taxonomic section, each species treatment is thorough. Included are the extensive listing of literature, generalized description, discussion of identification problems, review of forma, general statement of distribution based upon the literature, detailed citation of specimens supporting distribution in the region under investigation. This is followed by ecological analyses in terms of the habitat, substrate, chemical-physical factors (which include temperature, light intensity, and chemical composition; i.e., CaO and pH), phytosociological occurrence, and list of associations in which it occurs. Illustrations for each species are of the chart type, i.e., with the same details represented for all species and arranged in horizontal rows.

The work is an ambitious one, possibly suffering somewhat in being more extensive than intensive. Unfortunately, documentation of statements and specimens is sparse. For example, the author treats Soulat-Ribette's species, but fails to indicate where the specimens may be found. Unfortunately, too, he has perpetuated some of Hy's unorthodox nomenclatural practices, such as citing subspecies in the specific form; e.g., *Chara vulgaris* subsp. *Chara eu-vulgaris* Zanev. rather than the usual *Chara vulgaris* subsp. *eu-vulgaris* Zanev. In the taxonomic portion, the author could have checked original specimens more extensively. For instance, *Tolypella Palhinae* is treated in detail; yet, had the author seen the type, he would have found that it is not a *Tolypella* at all and has been annotated as a *Nitella* by both Mendes and Feldmann.

The text is printed on thin paper in small type, but the format is helpful and the utilization of varying type faces focuses attention on essential details. In all, the work is an invaluable contribution to our knowledge of Characeae.—R. D. WOOD, University of Rhode Island, Kingston.

NOTE

J. S. Canner & Company, Inc., 618 Parker Street, Boston-Roxbury 20, Mass., have reprinted BULLETIN OF THE TORREY BOTANICAL CLUB vols. 1–23, 1870–1896 on Microcards. These are available at $67.50 the set.

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COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF BRITTONIA

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